

# JOURNALOF HABILITATION

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### IN THIS ISSUE:

Using smartphones to track wildlife-vehicle collisions and improve data... Challenges facing the urban-dwelling raptor: are there enough resources to reproduce?... New Zealand and free-ranging cats: an island country rethinks an old problem.

#### **ABOUT THE JOURNAL**

THE Journal of Wildlife Rehabilitation is designed to provide useful information to wildlife rehabilitators and others involved in the care and treatment of native wild species with the ultimate purpose of returning them to the wild. The journal is published by the International Wildlife Rehabilitation Council (IWRC), which invites your comments on this issue. Through this publication, rehabilitation courses offered online and on-site in numerous locations, and an annual symposium, IWRC works to disseminate information and improve the quality of the care provided to wildlife.



On the cover:

Turtle in surgery to reattach fin after entanglement in a fishing net (Australia Wildlife Hospital). PHOTO ©WIETS?, FUCKR.COM. CREATIVE COMMONS LICENSE

#### Left:

White-tailed deer, fawn and adult (Odocoileus virginianus). PHOTO © CINDY CORNETT SEIGLE, FLICKR.COM. CREATIVE COMMONS LICENSE.



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#### EDITORIAL

## What Constitutes a Successful Release?

We measure our wildlife rehabilitation success by our release rates. How many of us stop to consider what makes a successful release?

*Location, location, location.* Location is an obvious factor in a successful release. It must be appropriate to the species and the animal's age. The challenge is to find a location with abundant recognizable foods and suitable shelter, but without undue hazards such as cars, poisons, and cats. The presence of conspecifics is often a requirement for a release site, but the rehabilitator must judge whether the habitat is already at its carrying capacity for a given species.

Many parameters of successful release come down to rehabilitator "preparedness" and the animal's health, age, and wildness. Some factors of health are easy to analyze: the X-ray shows a healed ulna, the parasite load is within acceptable limits, blood tests report a normal white blood cell count. More challenging is an analysis of the thrive factor. Is the animal in top condition, able to hunt or hide from predators with lighting reflex? Can it run or fly for long distances without evidence of weakness from the old wound?

A further challenge is deciding if an animal is at the appropriate age for release. Fortunately, this is an area where scientific papers and networking with other rehabilitators provide valuable data. Tree swallows are independent not long after fledging. Barn swallows are cared for by parents well through their first summer. Orphaned beavers need two years of care, while cottontail rabbits are released in mere months.

Waterproofing, food identification, hunting/foraging success, and wildness are other considerations. Of these, I find wildness the most challenging to determine. And, of course, wildness also intersects with age. At certain ages, a crow might seem hopelessly habituated despite your care to avoid interacting with it. But after another month of maturing, it acts with appropriate behavior and is ready for release.

There are always caveats, exceptions, and other considerations. Age doesn't always reflect ability to survive independently. Renesting and wild fostering are successful releases in my book. A threeweek-old squirrel or a brancher great horned owl might be successfully released if you follow best practices for renesting/ reuniting. Health is a trickier factor. Do you euthanize or release the three-legged deer? What about the Cooper's hawk that has that slight extension issue in its left wing?

Unfortunately, deciding whether an animal is ready for release, or should go back to the wild at all, is not just a black and white quantitative decision. You can use checklists and rate criteria, but in so many of our rehabilitation cases, the case requires a best judgment decision.

So do your best. Follow the accepted criteria and document results. Evidence and research will provide us with more knowledge and the ability to make a better decision next time. Work with scientists to develop post-release monitoring programs, or less formally work with citizen scientists on post-release observations as they spot the released black squirrel in their backyards.

Most of all continue to think, analyze, and question.

Kai Williams Executive Director

#### IN THE NEWS

#### New Saskatchewan Rescue Center

REGINA, Saskatchewan, Canada (July 16, 2014)—A non-profit organization, Salthaven West, has become the newest wildlife rescue center after opening its doors in Regina.

Since April, the organization's Megan Lawrence has cared for about 100 animals that were injured or found, as babies, and unable to fend for themselves. "Our goal is to release healthy animals back into the wild," Lawrence told CBC News Tuesday. "The animals that come into us are either too young or too sick to care for themselves."

There are rehabilitation centers for wildlife in Moose Jaw and Saskatoon which used to care for animals from the Regina area. In the past, however, the travel distance sometimes took a toll. With Salthaven West now open, there is another place to take sick and injured wildlife. It is also the first licensed rehabilitation center in Regina, Lawrence added, which means it has a permit for what is being done. "We take in reptiles, mammals, and birds," she said. "It's a very busy day, from about 7 a.m. to midnight when my day ends."

## Wildlife Hotline Launched in Georgia

TIFTON, Georgia, USA (July 7, 2014)— In an effort to educate the public about what to do when finding a wild animal that may be injured or orphaned, the Georgia Wildlife Rescue Association (GWRA) has released information about the numbers and types of calls that they have received on their statewide Wildlife Hotline. Barely two months old, the tollfree number has had even more of an impact than expected. Calls average 25 per day, but the organization reports receiving as many as 50 on some days.

GWRA director, Chet Powell, says that besides helping people find where to get help for wild animals, the best thing about the hotline is that it has actually prevented animals from being picked up unnecessarily. "People obviously mean well

#### IN MEMORIUM

#### Wilna Wilkinson

It is with great sadness that the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) and the conservation community bids farewell to Wilna Wilkinson, SANCCOB's Eastern Cape Rehabilitation Manager. Wilna tragically passed away in a car accident on Tuesday, 29 July 2014. She was a beloved member of the SANCCOB team, a brilliant advocate for penguins and the ocean, and a special friend to many people she met during her travels.

Wilna was appointed as Rehabilitation Manager of SANCCOB's center in Cape St. Francis in May 2013 after the facility (previously known as Penguins Eastern Cape) was amalgamated under SANCCOB's management. She played an instrumental role in setting up and running the new facility in Cape St. Francis and working together

with the various colony managers and conservation partners in the region. In addition, her involvement was pivotal during the Kiani Satu oil spill in August 2013 when the center admitted 277 oiled seabirds including African penguins, Cape gannets, and Cape cormorants. Under Wilna's management, the team successfully released 95% of the seabirds back into the wild.

In honor of Wilna, the SANCCOB team hosted a public beach release of rehabilitated Cape gannets. She was posthumously given an award of excellence to SANCCOB and to seabird conservation. SANCCOB extends its gratitude to all

its partners and friends in conservation around the world for their messages of condolence.



when they see a baby animal all alone, but we tend to forget that it's still a wild animal and not a human baby," said Powell. He added that before the hotline was implemented on May 1st, the GWRA had estimated that half of the calls to it would be "false rescues," where people had removed suspected injured or orphaned animals that were actually never in any danger at all. That estimate turned out to be low.

By asking people to call the hotline before picking up an animal, the GWRA is able to help educate the caller, and the end result is usually leaving or returning the animal to where it was found. "We were surprised to find that out of every five calls to the hotline, four resulted in the animal either being left where it was found or it was put back," he said. Powell expects that ratio to remain fairly consistent. The most frequent calls in May and June involved baby animals, especially deer, birds, and rabbits. Powell gave an example, "A person is walking on a trail or even in their neighborhood and sees a fawn, a baby deer, all alone and immediately assumes that it's an orphan and picks it up. That's not a rescue," says Powell, "that's a kidnapping. Deer leave their young alone for long periods during the day. It's just as normal and safe for them as a human baby is in a crib."

#### Walden's Puddle Starts Recovery Process

*JOELTON, Tennessee, USA (July 3, 2014)*—Walden's Puddle wildlife rehabilitation center continues its recovery efforts after the facility caught fire on June 23. At least 75 animals died as a result of the fire.

The fire appears to have been caused by a dryer that spontaneously combusted. A smoke detector installed in the laundry room has been credited with saving most of the animals. Cardboard now covers the window that employees broke to save birds in one room from smoke billowing in the hallway.

Most of the surviving animals have remained in temporary shelters on the property and some were moved offsite, as renovation efforts continue.

While center employees said they're grateful that so many animals were saved, they still mourn the ones that were lost. "We treasure each life. It's difficult . . . more and more people know about the greater good of this mission because of those animals," said Lane Brody, Walden's Puddle Board Chairman.

Walden's Puddle has established a donation fund to help them recover from the fire.

#### U.S. House of Representatives Supports Wildlife Rehabilitation

WASHINGTON, DC, USA (June 26, 2014)—The Humane Society of the United States (HSUS) praised the introduction of H. Res. 651, a Congressional resolution recognizing the important role experienced and accredited wildlife rehabilitation centers play in caring for native wildlife in communities across the country.

The resolution—sponsored by Rep. Lamar Smith, R-Texas—takes into account the important work of wildlife rehabilitators, who care for and release wildlife indigenous to the U.S., often on a voluntary basis.

Wayne Pacelle, president and CEO of the HSUS, said, "We applaud Representative Lamar Smith for recognizing the importance of wildlife rehabilitators across the nation—a network not as well developed as animal shelters, but just as important and vital for communities. The people working in this field, principally as volunteers, provide a remarkable safety net for wildlife facing an extraordinary set of risks, from cars to power lines to poisons."

The HSUS and its affiliates operate



Golden eagle (*Aquila chrysaetos*), a species commonly poisoned by lead shot.

three wildlife rehabilitation centers located in California, Florida, and Massachusetts that rescue, care for, rehabilitate, and eventually release back into the wild thousands of orphaned or injured wild animals from across the country every year. "There are hundreds of other centers that collectively provide help to hundreds of thousands of wild animals in crisis situations," added Pacelle.

Rep. Smith said, "I have enjoyed working with wildlife rehabilitation centers in my Congressional District. These organizations across our nation deserve our support. Every year, hundreds of thousands of wild animals are orphaned, injured, or become sick. This resolution recognizes the work of wildlife rehabilitation centers and their selfless efforts to protect our wildlife. Today, we thank these individuals and organizations for what they do on a daily basis."

#### Wildlife Organizations and Hunters Band Together

WASHINGTON, DC, USA (June 10, 2014)—Animal protection and wildlife conservation groups, along with individual hunters and sportsmen, have petitioned the Department of the Interior to require the use of non-lead ammunition when discharging a firearm on the more than 160 million acres of federal lands managed by the National Park Service and the U.S. Fish and Wildlife Service. Each year, an estimated 10 to 20 million birds and other animals die from lead poisoning, either by ingesting lead shot or fragments directly or by feeding on lead-contaminated prey.

Lead ammunition has been prohibited nationwide in waterfowl hunting since 1991, and hunters adapted to non-lead ammunition for the hunting of ducks, geese, and other waterfowl. More than 20 years later, the groups argue it's time to expand this sensible environmental policy to the hunting of big game, upland game birds, and other species on lands managed by the National Park Service and the U.S. Fish and Wildlife Service.

Andrew Wetzler, director of land and wildlife for the Natural Resources Defense Council, said, "We don't put lead in paint anymore. We don't put it in gasoline. Or even pencils. Why should we still allow it to poison the wildlife and wild places that Americans are so desperate to see? By allowing continued use of lead shot on public lands, that is essentially what is happening. Just like in the products we use daily, there are newer and better options for sportsmen to protect their health and the animals living on those landscapes they value."

The toxicity of lead to both human and environmental health is well documented. More than 500 scientific papers have cited the many dangers to wildlife caused by lead exposure. A single ingested shotgun pellet is sufficient to cause brain damage and organ failure in an animal, resulting in inhibition of critical neuromuscular, auditory, and visual responses. Lead poisoning can induce lethargy, blindness, paralysis of lungs and intestinal tract, seizure, and death. More than 130 species, including threatened and endangered wildlife, as well as iconic species such as bald and golden eagles, have been poisoned or killed by lead ammunition. The toxicity of lead ammunition also poses health risks to people who eat animals shot with lead ammunition.

Kai Williams, executive director of the International Wildlife Rehabilitation Council, said, "Wildlife rehabilitators are the first responders of the lead toxicity epidemic. One Wisconsin wildlife rehabilitation center reports up to 33 percent of bald eagle patients present with significant lead toxicity. Unfortunately, even more succumb to acute lead poisoning without ever reaching a wildlife hospital."

## Monitoring wildlife-vehicle collisions in the Information Age: How smartphones can improve data collection

Daniel D. Olson,<sup>1\*</sup> John A. Bissonette,<sup>1</sup> Patricia C. Cramer,<sup>1</sup> Ashley D. Green,<sup>2</sup> Scott T. Davis,<sup>3</sup> Patrick J. Jackson,<sup>1</sup> and Daniel C. Coster<sup>4</sup>



Red fox (Vulpes vulpes) on an overpass in Toronto.

#### Introduction

Wildlife-vehicle collisions (WVCs) are a global problem that impact both wildlife and motorists.<sup>1–5</sup> The sheer number of animals that are killed in vehicle collisions is alarming; in the United States alone, it has been estimated that ~1 million vertebrates are killed every day.<sup>6</sup> Wildlife-vehicle collisions involving large species, such as ungulates, can cause substantial vehicle damage and human injuries and, consequently, are a key public safety concern.<sup>7</sup> In the United States, there are 1–2 million vehicle collisions with large animals each year that result in \$8.4 billion (all currency values represent USD) in damages.<sup>8</sup> Additionally, ~5% of WVCs result in human injuries<sup>7.8</sup> and, in the USA, human fatalities resulting from WVCs have risen to ~200 annually.<sup>9</sup>

There is a current, critical need for accurate and standardized WVC data,<sup>10–12</sup> because these are the foundation for mitigation projects that protect both motorists and wildlife.<sup>13</sup> For example, exclusionary fencing (>2 m high) is used to prevent wildlife from accessing road right-of-ways, and it is typically only constructed on road sections with high traffic volumes and high numbers of WVCs.<sup>14</sup> Wildlife crossings, which promote connectivity and facilitate safe passage of wildlife above (overpasses, e.g., bridges, green bridges) and below (underpasses, e.g., culverts, tunnels, bridges) roads, are also placed in areas where WVCs occur.<sup>15–18</sup> Effective WVC mitigation is generally costly,<sup>19</sup> and high quality WVC data help ensure that limited mitigation resources are strategically targeted to areas that produce the greatest results for motorists and wildlife. However, effectively gathering ABSTRACT: There is a critical need for accurate and standardized wildlife-vehicle collision data, because it is the underpinning of mitigation projects that protect both drivers and wildlife. Collecting data of this magnitude requires an efficient data collection system. Currently, there is no widely adopted system that is both efficient and accurate. Our objective was to develop and test an integrated smartphone-based system for reporting wildlife-vehicle collision (WVC) data. The WVC Reporter system we developed consisted of a mobile web application for data collection, a database for centralized storage of data, and a desktop web application for viewing data. During the first year of use, 6,822 animal carcasses were reported using the WVC Reporter. The desktop web application improved access to WVC data and allowed users to easily visualize wildlife-vehicle collision patterns at multiple scales. The WVC Reporter integrated several modern technologies into a seamless method for collecting, managing, and using WVC data. As a result, the system increased efficiency in reporting, improved accuracy, and enhanced visualization of data. The development costs for the system were minor relative to the potential benefits of having spatially accurate and temporally current wildlife-vehicle collision data.

KEY WORDS: cell phones, data management, data reduction, highways, roads, Utah, web-based applications, wildlifevehicle collisions, smartphones, data collection, reporting wildlife-vehicle collisions, mobile web application, WVC Reporter

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Reprint: Olson *et al., PLoS ONE.* 2014; 9(6): e98613 doi:10.1371/journal. pone.0098613. ©2014 Olson *et al.* Creative Commons Attribution License. WVC data for mitigation planning has proven challenging<sup>12</sup> because WVCs occur over broad geographic areas, during all seasons of the year, and in large numbers.<sup>6,20</sup> Collecting data of this magnitude requires many observers and an efficient data management system.

Ecologists have been collecting WVC data since at least the 1920s.<sup>21</sup> These early ecologists recorded WVC data manually using the only method available to them at the time: pen and paper. Now almost a century later, many if not most state agencies still use the pen/paper method to report animal carcasses that occur on roadways.<sup>12</sup> This is problematic because data collected in this manner generally have low spatial accuracy (i.e., nearest highway/ marker), contain avoidable inaccuracies, and require a considerable time investment to reformat data digitally so that they are useful for analyses and mitigation planning.<sup>10</sup> For instance, data must be entered once on a paper form while in the field and then manually transcribed into an electronic database. After data are in an electronic database, they must then be imported into a Geographic Information System (GIS) to be visually analyzed for mitigation planning. Errors inevitably occur in the process, as humans enter and transcribe WVC data manually, particularly if the handwriting on the paper form is semi-legible. Location data also may be prone to data entry errors. For example, the nearest marker may not be visible from the carcass location or the road may not have any visible markers, making reporting an accurate location difficult or impossible.

Researchers have been aware of the difficulties associated with WVC data for many years and, as a result, have been actively developing new methods with the goal of improving accuracy and efficiency. As early as 2005, Ament et al.<sup>22</sup> developed a system in which observers used Personal Data Assistants (PDAs) to electronically record data on animal carcasses and to generate spatially accurate location coordinates using integrated Global Positioning System (GPS) technology. This system represented a breakthrough in WVC data collection because it not only increased location accuracy, it also standardized data collection and eliminated transcription errors. Donaldson and Lafon also used this PDA system in Virginia.<sup>23</sup> The use of PDAs, however, did not solve all WVC data collection problems, because PDAs still required the user to periodically transfer data from the PDA to a database for storage, which can be cumbersome when many users are reporting data across large geographic areas. Additionally, in about 2006, PDAs began to be replaced by smartphones as the technology of choice. Consequently, PDA reporting systems have not been widely adopted for WVC data collection.

Another reporting system for WVCs was developed by Hesse *et al.*<sup>24</sup> in 2007. Their system used an inexpensive (~\$100), but lesser known, device called the Otto-Driving Companion. This device was attached to the dashboard of the vehicle, and it allowed the motorist to report animal carcasses with the push of a button while driving. The system generated spatially accurate locations using GPS, but was limited by the number of species that could be reported. Again, WVC data had to be downloaded manually

from each device to a database for the information to be usable. While this represented another step forward in WVC data collection, the Otto-Driving Companion has not been widely adopted.

Most recently, a small number of states and provinces (California, Idaho, Maine, and British Columbia has developed web applications for reporting WVCs.<sup>25</sup> These web-based systems allow users to report animal carcasses by accessing a website where they enter location and species information. Some systems even allow users to upload photos of animal carcasses. The development of web applications for reporting WVC data is a significant advancement that standardizes data collection and eliminates transcription, but these systems have two important limitations: 1) users must have internet access, and 2) users must define carcass locations based on what they know about the road location. The requirement of internet access requires personal computer users to either record the data or remember it until they have access to their computer. Some web applications can be accessed with mobile devices, but they require mobile broadband internet which is incomplete in most states, especially in rural areas where many WVCs occur. Web applications also require users to define the locations of WVCs manually, so there is the potential for significant location error to occur. Most web applications now have built-in map viewers (e.g., Google Maps) that allow users to zoom to and select a location on the map, which makes defining the location relatively easy. However, location errors associated with this technique are unknown and largely dependent on the user.

Currently, there is no widely adopted WVC data collection system that is both efficient for users and accurate for geographic locations. Our intent was to create a data collection system that increased efficiency and accuracy, but also had the potential to be broadly accepted and used. We also wanted to create a system that seamlessly integrated WVC data collection, storage, and analysis. In this paper, we review the development and testing of the WVC Reporter. The WVC Reporter is a smartphone-based reporting system that combines a mobile web application for data collection, a centralized database for data storage, and a desktop web application for analyses.

#### Methods

#### Study Area

The WVC Reporter was developed and tested in Utah (219,807 km<sup>2</sup>), which is located in the southwestern United States. The Utah landscape is topographically diverse with elevations ranging from 663–4,413 m.<sup>26</sup> The climate for much of the state is considered semi-arid (127–381 mm precipitation annually), but high elevation areas can receive considerably more precipitation (>1,473 mm).<sup>27</sup> Three major ecoregions comprise the majority of the state: the Colorado Plateau, the Wasatch and Uinta Mountains, and the Central Basin and Range.<sup>28</sup> As a result, Utah is ecologically diverse and inhabited by a wide variety of plants and animals that are adapted to an array of habitats from salt desert shrub lands to alpine tundra.<sup>29</sup>

Utah is largely a rural state with 75% of the land area being

federally or state owned.<sup>26</sup> There are, however, several urban areas along the western front of the Wasatch Mountains in central Utah, where the majority of the state's 2.8 million residents lives.<sup>30</sup> According to the latest census estimate, Utah was the third fastest growing state<sup>31</sup> in the United States. Consequently, the state is rapidly becoming urbanized.<sup>32</sup> The growing human population has increased demand for transportation, and traffic volumes have doubled in the past 30 years (1980–2010).<sup>33</sup> In 2010, it was estimated that 42.8 billion km were driven on the state's 73,413 km of roads.<sup>33,34</sup>

Wildlife-vehicle collisions commonly occur in Utah and are a considerable public safety concern.<sup>35</sup> Most reported wildlife vehicle collisions in Utah involve mule deer (*Odocoileus hemionus*),<sup>35</sup> which is the state's most abundant wild large mammal.<sup>36</sup> Vehicle collisions with mule deer in Utah result in an average of \$7.5 million in damages each year.<sup>37</sup> Consequently, mitigation measures such as wildlife crossings and exclusionary fencing have been used to address the problem.<sup>38</sup>

#### WVC Data Collection

Surveys for wildlife carcasses using automobiles have been conducted systematically in Utah since at least 1998.<sup>39</sup> Automobile surveys were done by Utah Department of Transportation (UDOT) contractors. During the study, UDOT contractors were contractually obligated to drive ~2,800 km of roads twice a week (Monday and Thursday) throughout the year. UDOT contractor routes were selected because they had high numbers of WVCs. During surveys, UDOT contractors were required to remove all animal carcasses that were detected on the road surface, the median, and the road shoulder. They also were required to keep detailed records of the species removed and their locations. Removal ensured that carcasses were not double-counted in future surveys, because removed carcasses were transported away from roads by survey crews and deposited at local landfills. Utah Division of Wildlife Resources (UDWR) employees also reported and removed animal carcasses that occurred on roads other than those covered by UDOT contractors (A. Aoude, UDWR, personal communication). UDWR employees did not conduct systematic surveys, but reported carcasses opportunistically. Prior to implementation of the WVC Reporter system, both agencies recorded animal carcass data using the pen/paper method.

#### WVC Reporter System

The WVC Reporter system consists of three integrated components: 1) a mobile web application, 2) a database, and 3) a desktop web application (Fig. 1). The mobile web application was designed for in-field data collection. It allows the user to report information on wildlife carcasses using a smartphone. When reporting a wildlife carcass, the user simply clicks on the mobile web application bookmark and a report form opens. The report form contains a dropdown menu of wildlife species that are commonly encountered. If the species being reported is not available in the menu, it can be entered manually. The user also enters the



FIGURE 1. Flow of information through the WVC Reporter system. Using the WVC Reporter system, data are collected in the field using smartphones and a mobile web application. Collected data are then transferred via mobile broadband internet to a centralized database that is dynamically linked to a desktop web application where WVC locations can be viewed.

sex (male, female, or unknown) and age class (adult, juvenile, or unknown) of the animal. However, it is important to note that accurately identifying species, sex, and age class of animal remains depends on a variety of factors that include observer experience, animal species, and the physical condition of the carcass. Optional information that can be reported with the application includes a carcass fat measurement (an indicator of health in ungulates) and an ID number if the animal was involved in a research study and marked.

For each reported carcass, the mobile application generates a number of pieces of information automatically. For example, the mobile web application accesses the smartphone GPS and acquires coordinates (latitude/longitude) for the location. Coordinates are then used to determine the nearest highway and marker automatically. This eliminates all data entry errors associated with location information. The mobile web application also reports the user, time, and date. When the user is finished entering information in the report form, the send button transfers data via a mobile internet connection to the WVC Reporter database. If mobile internet service is unavailable, the information is stored in the phone cache until the next report is submitted.

The mobile web application is compatible with most iPhone<sup>®</sup> and Android<sup>®</sup> smartphones. Specific device requirements include iOS Safari 3.2+, Android Browser 2.1+, or Google Chrome 10.0+. The programming code for the mobile web application was written in HTML5, CSS, and JavaScript. The HTML5 geolocation Application Program Interface (API) was used to enable location data collection, and the application cache allows the mobile web application to be used even when there is no internet connection available. Programming for all components of the WVC Reporter was done by the Utah Automated Geographic Reference Center (AGRC). The programming code for the system is provided in Appendix S1.

The WVC Reporter database serves as the central repository for all reports that are submitted using the mobile web application. The database is dynamic and updated when reports are submitted through an ESRI ArcGIS Server Feature Service. The



FIGURE 2. WVC Reporter map viewer depicting spatial patterns in wildlife-vehicle collisions. Spatial patterns in wildlife-vehicle collisions can be efficiently analyzed at both broad (left image) and fine (right image) scale extents using the WVC Reporter map viewer.

database is an ESRI ArcSDE Geodatabase, and it is housed in a Structured Query Language (SQL) Server at the AGRC in Salt Lake City, Utah.

The desktop web application was designed to make it easier for planners, maintenance crews, and wildlife managers to use WVC data. To accomplish this, the web application serves as: 1) a map to view carcass locations at user defined scales, 2) a place to download current WVC data, 3) a way to enter carcass data manually, and 4) a link to the mobile web application. To map carcass locations, the desktop web application uses ESRI's ArcGIS Server and ArcGIS API for JavaScript. The web application is dynamically linked to the WVC Reporter database, so mapped carcass locations represent the most current data available. Rather than display all carcass locations on the map regardless of the spatial extent, the map viewer shows clusters of carcass locations as circles, where the size of the circle represents the number of carcasses in the area (Fig. 2). As one zooms in on specific locations within the state, the circles become progressively smaller and eventually disappear at smaller scale extents showing only the actual carcass locations. This provides an efficient means to see where WVC hotspots occur regardless of the scale extent the map is viewed at. Carcass locations also can be overlaid on one of seven different base maps. The high-resolution aerial imagery base map provides an excellent backdrop for analyzing WVC patterns, because landscape features such as vegetation, rivers, human developments, agricultural fields, and roads are clearly visible at smaller scale extents. Additionally, the terrain base map shades relief making topography appear three dimensional, which is helpful for viewing carcass location with respect to major topographic features such as drainages. To add additional context not available in the base maps, we included GIS layers for wildlife crossing locations, exclusionary fencing, marker locations, and management regions (UDOT and UDWR) that can be toggled on and off by the user. The map viewer also includes data filters (date, species, and management region) allowing the user to modify data to suit their specific needs. For fine-scale WVC analysis, users can also enter a highway number (e.g., US 6) and section (e.g., markers 210-213), and the map viewer will zoom to that location and summarize WVC data for that area (Fig. 2). Finally, the map viewer allows displayed data to be exported as a

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PDF, which provides the user with a way to share data or create figures for reports.

While the map viewer provides an efficient means to visualize WVC patterns, in some situations it may be desirable to perform more sophisticated spatial analyses (e.g., spatial clustering or autocorrelation indices). To facilitate this, the desktop web application allows the user to download the WVC Reporter database as either an ESRI shapefile or a dbf file. The shapefile is a common GIS format that allows a carcass location to be easy imported into GIS software where spatial analyses can be performed. The download function also respects the data filters in the desktop web application.

When designing the desktop web application, we realized not all agency personnel reporting WVC collision data would have access to smartphones and, consequently, some information would still be collected on paper forms. To address this situation, the desktop web application has a report form for manually entering carcass locations. It essentially functions the same as the mobile web application report form, with the exception that the user has to define the carcass location manually by either entering GPS coordinates (latitude/longitude or UTM), the highway/marker, or the street address. Once the location information is entered, the user is able to verify that the location information was correct by viewing the location on a built-in map viewer.

The final function of the desktop web application is to serve as a location to link to the mobile web application. Before field technicians can use the mobile application on their individual smartphones, they must first access the web application (https:// WVC.mapserv.utah.gov/WVC/desktop/index.php), click on the mobile app link, and then bookmark the location on their smartphone. The desktop web application was programmed using the same languages as the mobile application, and it works with nearly all commonly used web browsers (Internet Explorer 7+, Chrome, Firefox, and Safari).

#### Location Error

We tested the WVC reporter application using a Motorola Droid X<sup>®</sup> smartphone (Model 10083V2-B-K1, Verizon, New York, New York, USA) and an Apple iPhone 4<sup>®</sup> (Model A1349, Apple, Inc., Cupertino, California, USA). To estimate the horizontal error for locations collected with these phones, we tested them at random locations on highways throughout the state of Utah. At each random location, we recorded location coordinates using a mappinggrade Archer Differential Global Positioning System (DGPS) receiver (Model XF101, Juniper Systems, Logan, Utah, USA) that was capable of sub-meter accuracy. We used locations collected with DGPS receiver to represent the "true" location. Additionally at each random point, we recorded location coordinates using the smartphones and a recreation-grade Garmin' GPS receiver (Model eTrex Legend H, Garmin International, Inc., Olathe, Kansas, USA). We included the recreation-grade GPS in testing to determine how the smartphones compared to a standalone GPS receiver. All location data were imported into ArcGIS 10.1

(ESRI, Redlands, California, USA) for analysis. Location error was estimated as the Euclidean distance between the true location and the points collected by the test units. Because the location errors were not normally distributed, we reported the medians and median absolute deviations (MADs) instead of means and standard deviations. We also used the nonparametric Kruskal– Wallis test to test for differences in location errors between units. All statistical tests for this study were performed using R 2.14.1 (R Development Core Team, Vienna, Austria). To estimate how much spatial accuracy improved by using smartphones and WVC Reporter application, we compared location errors associated with that technique to those empirically measured by Gunson *et al.*<sup>10</sup> for reporting highway/marker locations. We used this information to estimate the percent decrease in location error associated with using smartphones and the WVC Reporter application.

#### Data Entry and Transcription Times

We estimated the amount of time required to report carcasses using the WVC Reporter application and the pen/paper method under field conditions. Data entry times can vary based on an individual's natural ability and experience level. To reduce this bias, all data entry times were collected by the principal investigator, who was experienced entering data using both the pen/paper method and the WVC Reporter application. Data entry and transcription times were recorded in seconds (s) using a stopwatch. For WVC Reporter, data entry times represented the time from when the application was opened on the smartphone until all data was entered and the submit report button was pressed. Data values entered included species, sex, and age class. For the pen/ paper method, data entry and transcription times represented the time from when the first and last data values were entered. Values entered included date, highway/marker, species, sex, age class, and GPS coordinates in UTMs. Data entry times were also non-normal, so we reported medians and MADs. We tested for differences in data entry times between methods using the Kruskal–Wallis test.

To determine how much time could be saved annually, we compared the annual data entry time for the WVC Reporter and the pen/paper method. We estimated annual data entry time for the WVC Reporter by multiplying the median data entry time for each smartphone by the number of carcasses reported during the first year (n = 6,822). Similarly, we calculated annual data entry time for the pen/paper method by multiplying the median data entry by the same number of carcasses (n = 6,822). We then subtracted annual data entry time for the WVC reporter for each phone to get the estimated range of hours saved by using the WVC reporter. A range was reported because the two smartphones tested had slightly different data entry times.

#### Data Entry Errors

We estimated reporting errors for the previous system of paper forms and transcription. Data used to estimate entry errors were collected and transcribed by UDOT contractors prior to the implementation of the WVC Reporter system. Due to the nature of the dataset, reporting errors could only be verified for location data. Errors undoubtedly occurred due to misidentification of species, sex, and age information for carcasses, but we did not evaluate these errors because it would have required a separate field study that would have exceeded the financial resources available for this project. Location data collected included highway/marker, and GPS coordinates in UTMs. To identity location errors in carcass records, we imported carcass locations into ArcGIS 10.1 and overlaid them on highway/marker locations to verify that the reported GPS coordinates matched the reported highway/marker locations. If GPS coordinates and highway/marker information matched, we assumed that both had been recorded correctly. When GPS coordinates were associated with a highway, but the reported highway/marker did not match that location, we assumed that the highway/marker was reported incorrectly. When GPS coordinates did not coincide with a highway, we assumed that the coordinates were reported incorrectly.

#### Cost Savings

To estimate the total cost savings from using the WVC Reporter, we used the data entry time saved for both in-field data collection and transcription and assumed the mean hourly wage for those reporting and transcribing data was USD\$12/hr.

#### Results

#### WVC Reporter System

We began development on the WVC Reporter in July of 2011. The system was thoroughly tested for a six-month period (October 2011-March 2012) prior to its release. Development costs for programming and testing totaled USD\$34,000. Annual maintenance costs were estimated to be USD\$1,500. The WVC Reporter officially went into use across Utah on April 16, 2012. Use of the WVC Reporter application was restricted to UDWR and UDOT personnel, UDOT contractors, and select wildlife and transportation professionals. During the first year of use, 6,822 carcasses were reported by 47 different users across the state. A total of 43 different species were reported, but the majority of carcasses (85%) were mule deer. However, it is important to note that carcass reporting was focused on medium to large mammals because those species posed the greatest threat to driver safety. Smaller species were likely underrepresented because they have lower detection rates and were not a substantial public safety concern.

Spatial patterns were also clearly apparent at multiple scales when using the map viewer to assess carcass locations. For example, the majority of WVCs statewide occurred in the north central portion of the state (Fig. 2). At the scale of individual highways, carcasses appeared to be clustered in hotspots along highways. At fine scale resolutions, the landscape and infrastructure features associated with hotspot locations were clearly visible when viewed in conjunction with a high-resolution aerial imagery (Fig. 2).

#### Location Error

Location error varied between the units we tested (K = 25.26, p<0.01). The Droid X had the highest median location error (5.2 m). The location error for the iPhone 4 was lower (4.6 m), but similar to the Droid X. The Garmin GPS had the lowest median location error (2.4 m). All units tested produced location data that could be used for precise spatial analysis and mitigation planning. When we compared location errors for data collected with smartphones using the WVC Reporter application to those associated with recording only highway/mile locations (= 401 m, SD = 219 m, reported by Gunson *et al.*<sup>10</sup>), we found that location error decreased 99% when using the WVC Reporter application. Using a Garmin GPS instead of the smartphones we tested would have further decreased location error <1% (Table 1).

#### Data Entry and Transcription Times

Data entry times varied between the methods we tested (K = 225.95, p = <0.01). Median entry times using WVC Reporter application (22.0–26.5 s) were 49–58% shorter than the median data entry time (52 s) for the pen/paper method (Table 2). We estimated that the WVC Reporter reduced data entry time by 48.3–56.9 hours per year in Utah.

The median transcription time for observations was 53 s (n = 114, MAD = 3.7, Range = 45–81). As the WVC Reporter completely eliminates manual transcription, we estimated that 100.4 hours were saved per year in Utah on transcription alone. However, it is important to note that transcription times can vary due the ability of the transcriptionist and care with which the original data were recorded.

#### Data Entry Errors

We measured data entry error rates for carcasses that were reported using the pen/paper method and then transcribed into an electronic database (Table 3). Data entry error rates were highest for marker locations (19%), intermediate for GPS coordinates (10%), and lowest for highway names (1%). The overall data entry error rate for all location data was 10%.

#### Cost Savings

Increased efficiency often translates into reduced costs for data collection and use. In Utah, we estimated that 148.7–157.3 hours of work were saved on entry and transcription of WVC data. As a result, it is possible that USD\$1,784–\$1,886 in labor costs were saved with the WVC Reporter system, using the assumption that labor costs USD\$12/hr. Additional cost savings almost certainly occurred because data management and analysis were streamlined by the WVC Reporter system, but those savings were not as easy to document and were not estimated in this study.

#### Discussion

In 2008, Bissonette and Cramer<sup>11</sup> recommended accurate and standardized WVC data as a priority for transportation planning and wildlife management in North America. Given the recent advances that have taken place in mobile communications and electronics, it seemed promising that WVC data collection could

be improved by incorporating these modern advances. The WVC Reporter was specifically designed to leverage modern technologies to produce accurate and standardized WVC data. The system accomplished this by integrating several modern advances (smartphones, GPS, a mobile application, mobile broadband internet, an electronic database, a web application, and a map viewer) into a seamless method for collecting, managing, and using data. The system was developed and tested statewide to serve as a proof of concept, but has the potential to be adopted throughout North America because it produced accurate data, improved efficiency, and enhanced data management and use.

Accuracy was increased by reducing errors associated with location data and by reducing data entry errors. On average, location error for the smartphones we tested was only -4-5 m and the largest recorded error for either phone was 23 m. However, location error for highway/marker method can be 800 m, even if locations are reported correctly.<sup>10</sup> Location error of that magnitude can potentially obscure relationships with vegetation, topography, and infrastructure that can be highly variable within an 800 m area. Alternatively, locations collected with smartphones were accurate enough that relationships with landscape features and infrastructure were readily apparent, providing managers with a clearer understanding of factors associated with WVCs at finer spatial scales. Additionally, patterns in WVCs can be influenced by broad scale landscape processes, such as seasonal changes that trigger long distance migrations of ungulates in temperate climates.<sup>40,41</sup> The seasonal flow of large numbers of migrating ungulates often results in peaks in WVCs in fall and spring.9,42 With accurate spatial data on WVCs during migration times, managers will be able to precisely place wildlife crossings at scaled<sup>43</sup> locations where highways intersect migration routes, preserving natural ecological processes and reducing vehicle collisions.

With WVC data that is both spatially accurate and temporally current, management can be conducted at a fine scale to address problems as they arise. For instance, deer are occasionally killed on roads that have exclusionary fencing. This can happen when fencing becomes damaged or gates are left open. If maintenance crews observe that deer carcasses are being reported in areas with exclusionary fencing over a short time period of days or weeks, they can examine the location for damaged fencing or open gates, allowing them to quickly address the problem while it is occurring to prevent further WVCs at that location. When WVC data are collected on paper forms, data can be months to years old before they are processed and examined. Subsequently, the opportunity to prevent WVCs is reduced. The WVC Reporter also improved data accuracy by reducing errors that occurred from data collection and transcription. When using the pen/method for data collection, ~10% WVC locations had associated errors. Errors occurred in highway names, marker locations, and GPS coordinates. The highest error rate occurred for marker locations (19%), which was likely due to the fact that markers were not always visible from carcass locations. GPS coordinates, which consist of a long string of numbers (e.g., 12 T 505698 4405622), were also prone to errors (10%) when collected and transcribed manually. Errors in GPS coordinates are especially problematic, because a seemingly innocuous error in which one digit is off by one number can make a location unusable. The errors that occur from manually recording and transcribing data were virtually eliminated using the WVC Reporter because location data were record by the mobile application using the smartphone's GPS capabilities, rather than by the user manually.

There was also a marked increase in efficiency when we compared the WVC Reporter system to the pen/paper method as data collection time was reduced 49-58% and transcription was eliminated. For one year of reporting in Utah, the time savings from these two factors alone equates to 2.5-4 weeks of work for one person. Time savings could be considerably more for states with higher numbers of WVCs. In one year, Pennsylvania had an estimated ~115,571 deer-vehicle collisions.44 If we assumed that these data were recorded with the WVC Reporter rather on paper forms, it is possible that 0.8-1.3 person-years of work could be saved. Today, state agencies are consistently asked to do more with fewer resources. They may not have the time or person power to process data that requires considerable labor to make it useable for management purposes. The use of WVC Reporter allowed managers to focus on analysis and planning rather than data entry and preparation.

Time savings produced by increased efficiency inevitably translates into reduced costs for agencies. We estimated that in one year \$1,784–\$1,886 were saved in data entry and transcription time in Utah. There are additional savings that occur in data management and analysis. A total of 47 state employees and contractors reported WVC data throughout Utah. Collecting data entry forms from all of those individuals at regular intervals is not trivial; it requires a considerable commitment of time and effort, which is not required with the WVC Reporter system. Additionally, data analysis is streamlined with WVC Reporter, because data do not have to be prepared for GIS analysis, and analysis time is reduced because data can be quickly viewed by simply accessing the desktop web application. These cost savings are more difficult to estimate, but are possibly equivalent to or exceed those costs saved on data entry and transcription.

The WVC Reporter had its own associated expenses. System development and testing was moderate (\$34,000). Additionally, annual maintenance costs (\$1,500) were 4.4% of the development costs. The WVC Reporter system also requires investment in smartphones and wireless data plans. These costs can be partially defrayed by the fact that many people already have smartphones, which would necessitate them only downloading the mobile application at no cost. When WVC Reporter costs are viewed in context of the problem, the investment in the system appears relatively minor. The average economic cost of a deer-vehicle collision has been estimated to be \$8,388 and as high as \$30,773 for a moose-vehicle collision.<sup>8</sup> Consequently only ~4 deer- vehicle collisions or ~1 moose-vehicle collision would need to be prevented to pay for system development. Additionally, if one human fatality

TABLE 1. Horizontal error (m) for locations collected with smartphones (Droid and iPhone) using the WVC reporter and a standalone Garmin GPS receiver.

LOCATION ERROR (m)							
UNIT	n	MEDIAN	MAD	RANGE			
DROID	60	5.2	4.5	0.7–23.2			
IPHONE	60	4.6	2.9	0.2–21.0			
GARMIN GPS	60	2.4	1.3	0.3-8.0			

Location errors were similar between the smartphones tested, but lower for the Garmin GPS. All units tested produced locations that would allow for precise mitigation planning.

TABLE 2. A comparison of entry times for data collected with the WVC Reporter application and the pen/paper method.

	DATA ENTRY TIME (s)						
METHOD	n	MEDIAN	MAD	RANGE			
WVC REPORTER (DROID)	111	22.0	5.9	10.0-42.0			
WVC REPORTER (iPHONE)	122	26.5	9.6	15.0-87.0			
PEN/PAPER (GARMIN GPS)	114	52.0	5.9	41.0-85.0			

Data entry times were 49–58% shorter when using the WVC Reporter application.

TABLE 3. Errors for location data that were collected using the paper/pen method and then transcribed into an electronic spreadsheet.

LOCATION DATA	n	ERRORS	% ERROR
HIGHWAY	1836	23	1.3
MILE MARKER	1836	356	19.4
EASTING COORDINATE	1836	196	10.7
NORTHING COORDINATE	1836	189	10.3
TOTAL	7344	764	10.4

Error rates were highest for mile markers, intermediate for GPS coordinates, and lowest for highway names.

could be prevented (estimated value of a human life is \$3.3–\$9.1 million<sup>8,45,46</sup>), the system would pay for itself many times over. While Departments of Transportation do not directly bear the majority of expense related to wildlife-vehicle collisions, they are mandated with improving road safety and are motivated to prevent wildlife-vehicle collisions, even though the financial benefits of mitigation (e.g., reduced vehicle repair and injury/fatality costs) do not necessarily return directly to the agency responsible for implementing the mitigation.

While the WVC Reporter has advanced data collection and use, the capabilities of the system could be expanded further. As most smartphones now have built in cameras, the mobile web application could easily be modified to allow users to submit photos of carcasses. Additionally, survey effort of users could be quantified by programming the mobile web application to track user's movements while they are conducting carcass surveys.

Quantifying survey effort allows for more rigorous analysis of WVC data. The WVC Reporter system could also be linked to a warning system for drivers. The warning system could be designed as a mobile application that notified drivers whenever they entered an area that was currently experiencing high numbers of WVCs. The alert produced by the warning system could also notify drivers if they are traveling during a time of day when WVCs are more likely to occur (e.g., evening or early morning). This form of warning system would provide drivers with the best information available on WVC conditions. P. W. Johnsen (personal communication) recently developed the AvoiDeer app for use in Norway (www.avoideer.com) for that purpose. Motorists download the AvoiDeer app and use it to record moose or other animals on the road. Other motorists with the app who approach the location are notified by sound and a visual signal on their phones that roadside wildlife have been sighted at the location. Given the effectiveness of the WVC Reporter in collecting location data, the system could easily be modified to record sightings of live wildlife, to collect data on wildlife crossing infrastructure, or for general maintenance issues like reporting potholes and broken/ missing road signs. The applications for this type of technology are broad and could potentially result in significant benefits for agencies, wildlife, and the public.

In just the past five years, citizen science has emerged as a powerful tool to address scientific problems that were previously too costly, difficult, or labor intensive for researchers to undertake.<sup>47</sup> Citizen science involves recruiting the general public to collect data for scientific research, and it has the power to focus the efforts of many individuals on large scale problems. WVCs are truly a large scale problem that affects much of the developed world.<sup>5,17,48</sup> The scope of the problem is beyond what can be addressed by agencies and researchers alone. For instance in Utah, 4% of the roads were surveyed for carcasses by contractors. Given the ease of data collection and management with the WVC Reporter system, it could easily be extended to a citizen science enterprise where the general public reported WVCs on roads that were not surveyed by agencies. Citizen science programs for WVC data collection have successfully been implemented in California (California Roadkill Observation System [CROS]), Maine (Wildlife Road Watch), and Idaho (Roadkill and Wildlife Salvage [RWS]) using web applications. The California system (CROS) uses citizens who can print an observation form from the website (http://www. wildlifecrossing.net/california/doc/add\_observation), record the information, and then enter the data on the web. Data include type of animal and/or species found, where and when located, how long it might have been dead, pictures of the roadkill, and any additional details about road or traffic conditions. The system then displays a summary of this information for different animal groups across the state. The Maine Audubon Wildlife Road Watch (WRW) also uses citizens to record roadside and road-killed animals (https://maineaudubon.org/wildlife-habitat/wildlife-roadwatch/). Observers create an account, and then add observations

of species by placing its location on a web-based map. Photos can be uploaded. The Idaho RWS does not require citizens to login or register (https://fishandgame.idaho.gov/species/roadkill/add) before reporting sightings of roadkills. The website provides entries for species killed, sex, and a box where observers can check their certainty of identification. This system also provides a web-based map where observers can pinpoint the location of their roadkill observation. Other optional data entries are possible, including whether the observer wants to salvage the animal, a species account box, and time of day, as well as observer personal information. Despite the challenges associated with citizen science programs (i.e., inexperienced observers, possible imprecise spatial locations, double reporting, people management), the expansion of WVC data collection to large scales will likely depend on the degree to which the general public can be leveraged using modern electronic reporting systems such as WVC Reporter. In summary, the WVC Reporter is a fully automated system that includes a mobile web application for data collection, a database for centralized storage of data, and a desktop web application for viewing data. Because the collection of location data is automated, the only source for error is species ID, sex, and age, and those are minor concerns for our system because only trained agency personnel report observations.

#### **Supporting Information**

#### Appendix S1

WVC Reporter programming code. (ZIP) doi:10.1371/journal.pone.0098613.s001

#### Appendix S2

Location errors. (CSV) doi:10.1371/journal.pone.0098613.s002

#### Appendix S3

Data entry times. (CSV) doi:10.1371/journal.pone.0098613.s003

#### Appendix S4

Transcription times. (CSV) doi:10.1371/journal.pone.0098613.s004

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#### **Literature Cited**

- 1. Ghamdi AS, AlGadhi SA. Warning signs as countermeasures to camel–vehicle collisions in Saudi Arabia. *Accident Analysis and Prevention.* 2004;36:749–760.
- Ramp D, Wilson VK, Croft DB. Assessing the impacts of roads in peri-urban reserves: road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. *Biological Conservation*. 2006;129:348– 359.
- 3. Mkanda FX, Chansa W. Changes in temporal and spatial pattern of road kills along the Lusaka-Mongu (M9) highway, Kafue National Park, Zambia. *South African Journal of Wildlife Research*. 2011;41:68–78.
- Noro M. Analysis of deer ecology and landscape features as factors contributing to deer-vehicle collisions in Hokkaido, Japan. Washington: Transportation Research Board. 15 p.
- Groot Bruinderink GWTA, Hazebroek E. Ungulate traffic collisions in Europe. *Conservation Biology*. 1996;10:1059– 1067.
- Forman RTT, Alexander LE. Roads and their major ecological effects. *Annual Review of Ecology and Systematics*. 1998;29:207–231.
- 7. Bissonette JA, Kassar CA, Cook JC. Assessment of costs associated with deer-vehicle collisions: human death and injury, vehicle damage, and deer loss. *Human-Wildlife Conflicts*. 2008;2:17–27.
- Huijser MP, McGowen PT, Fuller J, Hardy A, Kociolek A. Wildlife-vehicle collision reduction study: report to Congress. Bozeman: Western Transportation Institute. 232 p.
- Langley RL, Higgins SA, Herrin KB. Risk factors associated with fatal animal-vehicle collisions in the United States, 1995–2004. Wilderness & Environmental Medicine.

2006;17:229–239.

- Gunson KE, Clevenger AP, Ford AT, Bissonette JA, Hardy A. A comparison of data sets varying in spatial accuracy used to predict the occurrence of wildlife-vehicle collisions. *Environmental Management*. 2009;44:268–277.
- Bissonette JA, Cramer PC. Evaluation of the use and effectiveness of wildlife crossings. Washington: National Cooperative Highway Research Program, Transportation Research Board, National Research Council. Report 615. 2008. Available: http://onlinepubs.trb.org/onlinepubs/ nchrp/nchrp\_rpt\_615. pdf. Accessed 2013 April 25.
- 12. Huijser MP, Wagner ME, Hardy A, Clevenger AP, Fuller JA. Animal-vehicle collision data collection throughout the United States and Canada. Washington: Transportation Research Board. 2007. 108 p.
- 13. Ford AT, Clevenger AP, Bennett A. Comparison of methods of monitoring wildlife crossing-structures on highways. *Journal of Wildlife Management*. 2009;73:1213–1222.
- 14. Clevenger AP, Chruszcz B, Gunson KE. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin.* 2001;29:646–653.
- 15. Clevenger AP, Waltho N. Factors influencing the effectiveness of wildlife underpasses in Banff, Alberta, Canada. *Conservation Biology*. 2000;14:47–56.
- 16. Seiler A. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology*. 2004;10:301–313.
- van der Grift EA, Pouwels R. Restoring habitat connectivity across transport corridors: identifying high-priority locations for de-fragmentation with the use of an expert-based model. *In*: Davenport PJ, Davenport JL, editors. The Ecology of Transportation: Managing Mobility for the Environment. Environmental Pollution. Netherlands: Springer; 2006. p. 205–231.
- Gagnon JW, Dodd NL, Ogren KS, Schweinsburg RE. Factors associated with use of wildlife underpasses and importance of long-term monitoring. *Journal of Wildlife Management*. 2011;75:1477–1487.
- Huijser MP, Duffield JW, Clevenger AP, Ament RJ, McGowen PT. Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: a decision support tool. *Ecology and Society*. 2009;14:15.
- 20. Trombulak SC, Frissell CA. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*. 2000;14:18–30.
- 21. Stoner D. The toll of the automobile. *Science*. 1925;61:56–57.
- 22. Ament R, Galarus D, Richardson H, Hardy A. Roadkill observation collection system (ROCS). Bozeman: Western Transportation Institute. 2007. 65 p.
- 23. Donaldson B, Lafon N. Personal digital assistants to collect data on animal carcass removal from roadways. Transportation Research Record: *Journal of the Transportation Research Board*. 2010;2147:18–24.

- 24. Hesse G, Rea RV, Klassen N, Emmons S, Dickson D. Evaluating the potential of the Otto Wildlife GPS device to record roadside moose and deer locations for use in wildlife vehicle collision mitigation planning. *Wildlife Biology in Practice*. 2010;6:1–13.
- Lee T, Quinn MS, Duke D. Citizen, science, highways, and wildlife: Using a web-based GIS to engage citizens in collecting wildlife information. *Ecology and Society*. 2006;11:11.
- Leydsman McGinty EI. Land ownership of Utah. *In*: Banner RE, Baldwin BD, Leydsman McGinty EI, editors. Rangelands Resources of Utah. Logan: Utah State University Cooperative Extension Service. p. 9–23.
- Gillies RR, Ramsey RD. Climate of Utah. *In*: Banner RE, Baldwin BD, Leydsman McGinty EI, editors. Rangelands Resources of Utah. Logan: Utah State University Cooperative Extension Service. 2009. p. 39–45.
- Griffith GE, Omernik JM. Ecoregions of Utah (EPA). *In*: Cleveland CJ, editor. Encyclopedia of Earth. Washington: Environmental Information Coalition. 2009. Available: http://www.eoearth.org/article/Ecoregions\_of\_Utah\_ (EPA). Accessed 2013 May 11.
- 29. Welsh SL, Atwood AN, Higgins LC, editors. A Utah flora. Provo: Brigham Young University. 1993. 986 p.
- 30. Economic Research Service (2013) State Fact Sheets: Utah. United States Department of Agriculture. Available: http:// www.ers.usda.gov/data-products/state-fact-sheets/state-data. aspx?StateFIPS=49&StateName=Utah#. UdsyAUHCZ8F. Accessed 2013 Jul 8.
- U.S. Census Bureau. Resident population data. 2010. Available: http://www. census.gov/2010census/data/. Accessed 2013 Apr 25.
- 32. Leydsman McGinty EI. Urbanization in Utah. *In*: Banner RE, Baldwin BD, Leydsman McGinty EI, editors. Rangelands Resources of Utah. Logan: Utah State University Cooperative Extension Service. 2009. p. 153–156.
- UDOT. Vehicle miles of travel. Utah Department of Transportation. 2010. Available: http://www.udot.utah. gov/. Accessed 2013 Apr 25.
- Pope C, McEwan A. 2012 UDOT annual statistical summary. Salt Lake City: Utah Department of Transportation. 2012. 23 p.
- West PW. UDOT wildlife and domestic animal accident toolkit. Salt Lake City: Utah Department of Transportation. 2008. 67 p.
- Bernales HH, Hersey KR, Aoude A. Utah big game annual report 2011. Salt Lake City: Utah Division of Wildlife Resources. 2011. 220 p.
- 37. Bissonette JA, Kassar CA, Cook JC. Assessment of costs associated with deer-vehicle collisions: human death and injury, vehicle damage, and deer loss. *Human Wildlife Conflicts*. 2008;2:17–27.
- 38. Cramer P. Determining wildlife use of wildlife crossing structures under different scenarios. Logan: Utah State

University. Report UT-12.07. 2012. Available: http://trid. trb.org/view.aspx?id = 1147953. Accessed 2013 Jul 8.

- Bissonette JA, Rosa S. An evaluation of a mitigation strategy for deer-vehicle collisions. *Wildlife Biology*. 2012;18:414– 423.
- 40. Sawyer H, Kauffman MJ, Nielson RM, Horne JS. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*. 2009;19:2016–2025.
- 41. Sawyer H, Lebeau C, Hart T. Mitigating roadway impacts to migratory mule deer–a case study with underpasses and continuous fencing. *Wildlife Society Bulletin*. 2012;36:492–498.
- 42. Hubbard MW, Danielson BJ, Schmitz RA. Factors influencing the location of deer-vehicle accidents in Iowa. *Journal of Wildlife Management*. 2000;64:707–713.
- 43. Bissonette JA, Adair W. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation*. 2008;141:482–488.
- State Farm. Deer collisions increase, WV #1 again, Arkansas #9 nationally. State Farm Insurance Company. 2012. Available: http://www.statefarm.com/aboutus/\_pressreleases/2012/deer-crash-rankings-ar. Accessed 2013 Apr 29.
- 45. Lefler N, Fiedler R, McGee H, Pollack R, Miller J. Market analysis of collecting fundamental roadway data elements to support the highway improvement program. Washington: United States Department of Transportation, Federal Highway Administration. 2011. 41 p.
- 46. Sinha P, Braun F. Regulatory impact analysis (RIA) for existing stationary compression ignition engines NESHAP. Research Triangle Park: United States Environmental Protection Agency. 2010. 147 p.
- 47. Gura T. Citizen science: amateur experts. *Nature*. 2013;496:259–261.
- Conover MR, Pitt WC, Kessler KK, DuBow TJ, Sanborn WA. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin*. 1995;23:407–414.

## Hard times in the city-attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey

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Eurasian kestrel (Falco tinnunculus).

#### Introduction

Rapidly increasing urbanization is a global phenomenon that affects not only humans but also animals and plants.<sup>1</sup> While native biodiversity often declines,<sup>2</sup> urbanization promotes the biotic homogenization of species assemblages.<sup>3-5</sup> Because of the loss of natural habitat, urbanization generally leads to a complete restructuring of vegetation and species composition and has, thus, become a major concern in conservation biology.<sup>6,7</sup>

The urban environment can induce dramatic changes in animal behavior, physiology, and life-history.<sup>8–11</sup> Within species, studies on passerines have shown that urban individuals have smaller clutches that are generally laid earlier and that their nestlings are lighter than those of their rural conspecifics.<sup>12</sup> Ultimately, species able to adapt to the challenges posed by increasing urbanization will persist and may even increase, while those that cannot will decline or disappear. Urbanization thus filters bird communities (review in Shanahan<sup>13</sup>).

The success of urban species appears to be a function of the time since they initially colonized urban areas.<sup>14</sup> The most highly urbanized areas are dominated by "urban exploiters,"<sup>15,16</sup> a small number of mainly non-native species, especially nearctic passerines,<sup>17</sup> whose success in urban areas is largely related to their ability to exploit human

#### ABSTRACT

Urbanization is a global phenomenon that is encroaching on natural habitats and decreasing biodiversity, although it is creating new habitats for some species. The Eurasian kestrel (*Falco tinnunculus*) is frequently associated with urbanized landscapes, but it is unclear what lies behind the high densities of kestrels in the urban environment.

Occupied nest sites in the city of Vienna, Austria, were investigated along a gradient of urbanization (percentage of land covered by buildings or used by traffic). Field surveys determined the abundance of potential prey (birds and rodents), and the results were compared to the birds' diets. A number of breeding parameters were recorded over the course of three years.

High breeding densities in urban habitats do not necessarily correlate with high habitat quality. The high density of kestrel nests in the city center is probably due to the ready availability of breeding cavities. Highly urbanized areas in Vienna are associated with unexpected costs for the city-dwelling raptor, in terms both of prey availability and of reproductive success. The kestrel appears to be exploiting the urban environment but, given the poor reproductive performance of urban kestrels, it is likely that the species is falling into an ecological trap.

**KEYWORDS:** diet choice, ecological trap, *Falco tinnunculus*, historical building structure, nest site choice, nest survival, prey availability, urban exploiter, urban gradient

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**FIGURE 1.** Urban study area (243 km<sup>2</sup>) in Vienna, Austria. The urban gradient, displayed from black to grey (white, unsealed soil outside the study area), and occupied nest sites of *Falco tinnunculus* during the study period (2010–2012).



**FIGURE 2.** Sealed soil (%) and nearest neighbor distance (NND) between occupied nest sites of *Falco tinnunculus* in the study area in Vienna, Austria.

resources such as garbage dumps, feeders, and nest boxes.<sup>18</sup> Many other species are also found in the centers of large cities, although it is often hard to determine whether they are benefitting or suffering from the urban environment. It is conceivable that the decision to breed in highly urbanized areas might be based on a mistaken assessment of the quality of the environment, with individuals in urban centers suffering from a lower availability of food and lower breeding success. In such cases, the species is said to have fallen into an "ecological trap".<sup>19</sup>

The Eurasian kestrel (*Falco tinnunculus* Linnaeus, 1758) is clearly affected by urbanization. It was first recorded breeding

in urban environments in the latter half of the 19th century<sup>20</sup> and is now commonly associated with urbanized landscapes.<sup>21</sup> A number of studies have been performed on the diet and breeding success of urban kestrels,<sup>22–27</sup> but it is difficult to draw general conclusions from them, as each metropolis provides a unique habitat, differing from others in terms of size,<sup>28</sup> building structure,<sup>29</sup> and composition of vegetation.<sup>30,31</sup> Despite the previous work, it is still unclear whether the kestrel is a true urban exploiter or whether instead the urban environment represents an ecological trap for the species. The issue can best be addressed by analyzing the breeding success of members of an urban population that is sufficiently large to permit the comparison between "city-dwellers" and birds living in the suburbs.

The urban study area in Vienna  $(243 \text{ km}^2)$ , Austria, has the highest

documented density of Eurasian kestrels in a non-colonial urban breeding population,<sup>32,33</sup> c.f. <sup>22–27</sup> and is ideally suited to a study of this kind. We compared the species' biology along an urban gradient, defined by the density of buildings and areas used by traffic.<sup>34</sup> We considered (1) whether the breeding density of kestrels in urbanized landscapes results mainly from the availability of nest sites, based on the historical building structure, and asked (2) whether the use of the urban habitat is associated with differences in annual reproductive rates or (3) a sex bias in nestling survival. We also (4) analyzed causes of nest failure and tested whether (5) there is a link between breeding density, reproductive success, and availability of prey. Because of the data structure and the relatively small sample size, we pooled the nests investigated more closely into three defined urban zones, using the different zones as discrete explanatory variables (6) to examine the main categories of prey in the kestrels' diet and (7) to relate the diet to the availability of prey.

#### Results

#### Nest site choice and nest site availability

The kestrel monitoring in 2010 found a total of 251 occupied nests, while, in 2011, 297 nests and, in 2012, 215 nests were found (Fig. 1). The figures translate to a breeding density of 89–122 breeding pairs per 100 km<sup>2</sup> in urbanized areas of Vienna. Kestrels predominantly breed in building cavities (69%, based on nests occupied in 2010), where they largely use roof openings (41%). Abandoned crow nests in trees are less frequently used (18% of broods). In rare

cases, nest boxes (6%; 33 nest boxes were offered in the city) or window boxes (4%) are used.

The nearest neighbor distance (NND) decreases significantly with an increasing percentage of sealed soil (measured in a circle of radius r = 500 m around the nest site, Pearson Correlation, N (2010) = 251, r = 0.47, P < 0.001, Figs. 1 and 2). An analysis of microhabitat variables showed that the structure of buildings with nest sites differed significantly from those of buildings selected at random (Table 1). Unobstructed roof openings and the availability of green courtyards are more frequent at nest sites than at randomly chosen buildings. Accessible roof openings in buildings chosen at random are only found in the historical city center with a soil sealing factor of more than 52%.

Unlike their conspecifics in some other European cities (e.g., Davolová,<sup>22</sup> Romanowski,<sup>25</sup> and Riegart<sup>35</sup>), kestrels temporarily leave Vienna during winter and return in spring. The dates when kestrels arrived at their nest sites differed only slightly along the urban gradient (Table 2, P = 0.06).

TABLE 1. Habitat differences between buildings chosen at random (N = 240) and nest sites (N = 195) on buildings shown with a GLM with binomial error structure (random point = 0, nest site = 1) and a logit link function

VARIABLE	ESTIMATE	SE	T-VALUE	P-VALUE	SIGN.
INTERCEPT	-3.11	0.70	-4.46	< 0.0001	***
ROOF-OPENINGS [OPEN=1, CLOSED=0]	4.12	0.50	8.29	< 0.0001	***
FAÇADE [SMOOTH=0, NOT SMOOTH=1]	-0.46	0.26	-1.79	0.07	•
NEST HEIGHT / HEIGHT OF THE ATTIC [M]	0.29	0.10	3.22	0.002	**
<b>GREEN COURTYARD</b> [YES = 1, NO = 0]	0.88	0.27	3.33	<0.001	***

Significance codes: "\*\*\*" 0.001, "\*\*" 0.01, "•" <0.1.

TABLE 2. Dependence of breeding time (2010–2012) on the urban gradient (measured as percentage of sealed soil in r = 500 m around the nest site) and nearest neighbor distance (NND) as fixed effect in a generalized linear mixed model (GLMM)

BREEDING TIME	ESTIMATE	SE	T-VALUE	PR(> T )	EXPL.DEV.(%)	SIGN.
ARRIVAL DATE‡ ( <i>N</i> = 333)						
SEALED SOIL	-12.36	6.47	-1.91	0.0568	54.74	•
NND†	-2.49	2.90	-0.86	0.3920	13.85	NS
(INTERCEPT)	272.53	14.33	19.01	<0.0001		***
LAYING DATE‡ ( <i>N</i> = 157)						
SEALED SOIL	7.95	6.79	1.17	0.2440	40.68	NS
(INTERCEPT)	28.53	4.86	5.85	<0.0001		***

The nest site ID and the study year were included as random factors. The error family was chosen according to the type of response variable as Gaussian family and identity link function.

Explanatory deviance (in %) is given for each fixed effect. Note: "<sup>‡</sup>" data presented as residuals with the study year, "<sup>†</sup>" log transformed.

Significance codes: "\*\*\*" 0.001, " $\bullet$ " <0.1, "NS" not significant.

P = 0.06).

In 2010, kestrels arrived at breeding sites in the city center on average 3 days ( $\pm 3.7$  SD) earlier than at sites in suburban areas, and in 2011 the difference was 7 days ( $\pm 5.0$  SD). Males usually occupied nest sites before females, but the arrival dates of the two sexes overlapped.

# Breeding success and nestling survival along the urban gradient

There was no obvious effect of the urban gradient on the laying date (Table 2). The ratio of eggs hatched and the sizes of fledged broods depended upon the percentage of sealed soil and the laying date, both of which significantly decreased towards the city center and for later broods (Table 3). Differences in urbanization and laying date were sufficient to account for 32% of the variance (R2 for GLMM) in breeding success (number of fledglings). The clutch size and the fledging rate were significantly influenced by the laying date, with fewer eggs and fewer fledged hatchlings in later nests (Table 3). The mean values and SD for the breeding data are given in Additional File 1.

We found a primary sex ratio of 47% female and 53% male

offspring (variation from hypothesized 1:1 ratio, N = 71 broods, exact binomial test 2011: P = 0.82; 2012: P = 0.22), whereas the sex ratio at fledging was 54% female and 46% male (N = 91 broods, 0.23 < P < 0.33). Female offspring have a slightly higher rate of survival; of the chicks lost as nestlings (N = 54 individuals), 31% were females and 69% were males ( $\chi^2 = 3.84$ , P = 0.05).

#### Causes of nest failure

The initial fixed–effects model of nest survival included laying date and the percentage of sealed soil (Table 4). The best model shows daily survival rates decreasing with percentage of sealed soil from the suburbs towards the city center and with later laying dates. As there was only a slight difference from the model that includes the age of the nestlings when the nest was found, we are confident that the results are not biased by when breeding was confirmed (during incubation or during the nestling phase). We tested for the influence of NNDs on nest failure, as reproductive performance is expected to decline with increasing population density, but the resulting model did not meet the criteria for good candidate models. To test tolerance against a potential anthropo-

TABLE 3. Dependence of breeding parameters (2010-2012, N = 157) on the urban gradient (measured as percentage of sealed soil in r = 500 m around the nest site) as fixed effect in a generalized linear mixed model (GLMM)

BREEDING PARAMETER	ESTIMATE	SE	Z-VALUE	PR(> Z )	R2 FOR GLMM	SIGN.
CLUTCH SIZE ( N = 138)					4.5	
LAYING DATE‡	-0.01	0.00	-2.48	0.0132		*
(INTERCEPT)	1.54	0.04	38.80	<0.0001		***
HATCHING RATE					15.44	
LAYING DATE‡	-0.04	0.01	-2.94	0.0033		**
SEALED SOIL	-2.40	1.07	-2.23	0.0255		*
(INTERCEPT)	2.54	0.78	3.24	0.0012		**
FLEDGING RATE					16.04	
LAYING DATE‡	-0.04	0.02	-2.06	0.0399		*
SEALED SOIL	-2.13	1.25	-1.71	0.0882		•
(INTERCEPT)	2.60	0.99	2.62	0.0087		**
FLEDGED BROOD SIZE					32.31	
LAYING DATE‡	-0.02	0.00	-4.54	<0.0001		***
SEALED SOIL	-0.85	0.34	-2.48	0.0131		*
(INTERCEPT)	1.26	0.25	5.04	<0.0001		* * *

The nest site ID and the study year were included as random factors. The error family was chosen according to the type of response variable.

Note: "‡" data presented as residuals with the study year.

Significance codes: "\*\*\*" 0.001, "\*\*" 0.01, "\*" 0.05, "•" <0.1.

TABLE 4. Summary of model-selection according to Mark106 for fixed-effects models of daily survival rate for kestrel nests (N = 157)

MODEL	к	AICC	ΔΑΙCC	ΩI
LAYING DATE‡+SEALED SOIL (%)	3	271.42	0.00	0.5659
LAYING DATE‡+SEALED SOIL (%)+AGE FOUND	4	272.19	0.77	0.3852
LAYING DATE <sup>‡</sup>	2	276.61	5.19	0.0422
DISTANCE (M)† FROM CLOSEST OPEN GREEN SPACE (≥1 ha)+SEALED SOIL (%)	3	282.05	10.62	0.0028
PRESENCE/ABSENCE OF GREEN COURTYARD +SEALED SOIL (%)	3	282.88	11.45	0.0018
SEALED SOIL (%)	2	283.86	12.44	0.0011
AGE FOUND + SEALED SOIL (%)	3	284.89	13.47	0.0007
NEAREST NEIGHBOR DISTANCE (m) <sup>†</sup>	2	288.30	16.88	0.0001
AGE FOUND	2	290.46	19.04	0
INTERCEPT-ONLY MODEL (CONSTANT DAILY SURVIVAL RATE)	1	290.49	19.07	0
TIME TREND	2	290.89	19.47	0
TRAFFIC AREA ( $M^2$ , IN r=100 m AROUND THE NEST SITE) <sup>†</sup>	2	291.27	19.85	0

genic stressor, we incorporated areas used by traffic in one model but, in contrast to the observations on American kestrels (*Falco sparverius*),<sup>36</sup> we found no correlation.

A total of 33% of nests failed, with no statistically significant

differences between years (Kruskal-Wallis  $\chi^2_{(2,157)} = 2.06$ , P = 0.36). 83% of nest failures occurred during incubation, with 27% of failures connected to predation as confirmed by direct observation (Table 5) and 29% due to nest desertion. Hooded crows (*Corvus cornix*) and Carrion crows (*Corvus cornix*) and Carrion crows (*Corvus corne*) are both common in Vienna, but we found no significant difference in the abundance of these potential nest predators along the urban gradient (Z = 0.76, P = 0.45).

#### Availability of prey

No significant relationship was found between abundance of prey and breeding success. Neither the number of prey-sized birds nor the abundance of rodents was able to predict the occurrence of successful breeders (GLM with proportion of successful nests per transect as dependent variable with binomial error distribution and logit link function<sup>37</sup> and both average numbers of birds and rodents as two predictors in the model, N = 25transects, P for all predictors was not significant; birds: Z = 1.13, P =0.25; rodents: Z = 0.42, P = 0.42).

The abundance of prey-sized species of bird varies with location along the urban gradient. No difference was found for thrush-sized birds (GLM with urban zone as predictor variable Z = 0.91, P = 0.36), but sparrow-sized birds were more abundant in suburban areas (Z = 11.08, P < 0.001) and pigeons—which our pellet analysis confirmed were included in kestrels' diet—were more abundant in the city center (Z = 3.49, P < 0.001).

The rodent survey included 2,676 trapping events (N = 129 individuals) and caught almost exclusively field mice of the genus

Apodemus (98.4% of three species, A. sylvaticus, A. flavicollis, and A. uralensis), with very small numbers of house mice Mus musculus, brown rats Rattus norvegicus, and bank voles Clethrionomys glareolus, recorded. In view of the relatively minor importance of

field mice in the diet of urban kestrels (see Table 2) and of the small sample size, an analysis of the trapping data by urban zone was not undertaken. Of the species trapped in the survey, only the bank vole is active by day,<sup>38</sup> so the results indicate that diurnal rodents are hardly available in the city. The situation is in stark contrast to the surrounding areas, where diurnal voles (especially *Microtus arvalis*) are common.<sup>39,40</sup>

#### Diet choice in three urban zones

Pellet analysis showed no difference in the proportions of the main categories of prey between years (Kruskal-Wallis  $\chi$ 2-test: 0.22, P<0.62). There were differences between urban zones: pellets in the city center (N = 18 nest sites) consisted of 48.5% (by biomass, for details of calculation, see Methods) mammals, 39% birds, 3.5% reptiles, and 9% insects, while pellets found in the mixed zone (N = 10 nest sites) consisted of 56.6% mammals, 29.8% birds, 1.5% insects, and 12.1% reptiles. The pellets found in suburban areas (N = 9 nest sites) showed 79.6% mammals, 12.2% birds, 4% insects, and 4.2% reptiles. We could not identify all pellet contents to the species level, but 70.4% of small mammals that could be identified were Microtus arvalis voles (sub-sample size: N = 152 individuals). Other mammal species identified were 13.0% field mice (*Apodemus* spp.) and 8.3% shrews (*Soricidae*).

The ratio of pairs that preyed mainly on mammals as opposed to on birds (based on the estimated biomass per nest site) differed significantly between urban zones (mammals: Kruskal-Wallis  $\chi^2_{(2)}$  = 7.54, *P* = 0.02 and birds:  $\chi^2_{(2)}$  = 7.24, *P* = 0.03), as did Levin's index for breadth of diet, which was highest in the city center (Kruskal-Wallis  $\chi^2_{(2)}$  = 8.34, *P* = 0.02; Levin's index in the city center: 4.02, mixed zone: 3.10 and suburban area: 1.44). Reptiles were preyed upon more often in the mixed zone (Kruskal-Wallis  $\chi^2_{(2)}$  = 5.67, *P* = 0.06), while insects were taken at approximately equal amounts in all urban zones (Kruskal-Wallis  $\chi^2_{(2)}$  = 0.61, *P* = 0.74).

#### Discussion

#### Choice and availability of nest site

Nearest neighbor distances (NND) decreased with increasing percentage of sealed soil (Fig. 2), but pairs in the city center had lower reproductive success, measured in terms of hatching rates and sizes of fledged broods, than pairs in suburban areas. As falcons do not construct nests themselves, their breeding locations are limited by the availability of potential nest sites.<sup>41,42</sup> The correlation between the number of nest sites and the number of roof openings (Table 1) supports the notion that more kestrels breed in the city center due to the greater availability of building cavities. This can be attributed to the structural element of roof openings, which are limited to historical buildings in the city. Many species rely on environmental cues for a rapid assessment of habitat quality, thereby reducing the time and cost of finding a suitable breeding site.<sup>43–45</sup> In environments that have been altered, the use of cues that were formerly reliable might lead to reduced reproduction, turning these environments into ecological traps.<sup>19</sup> Most ecological traps have an anthropogenic origin<sup>46</sup> and migratory species might be more likely to fall into ecological traps created by urban landscapes;<sup>47</sup> compared to residents, migratory birds have more stringent time constraints in assessing the quality of breeding sites.<sup>44,48,49</sup> Early arriving individuals usually have preferential access to the best sites and partners, while later arrivals must settle in territories of progressively lower quality.<sup>50,51</sup> For territorial birds such as the kestrel, this should result in a sort of ideal-despotic distribution<sup>52</sup> where males first occupy the best sites, with poorer sites occupied successively later. We would expect the territories occupied first to show the highest breeding success, but our study revealed the opposite to be the case. Kestrels breeding in the center of Vienna tended to arrive before their suburban conspecifics (Table 2), suggesting that inner-city sites are assessed as being of at least equal quality. However, there were no differences in laying dates along the urban gradient and breeding performance (Table 3) was worse in inner-city districts than in the outskirts. Thus, the first returning kestrels do not select the best breeding sites. Breeding in highly urbanized areas was associated with higher rates of nest failure. Our models of nest survival showed that the percentage of sealed soil and the laying date are the main variables connected to nest failure (Table 4). A close proximity to large open green spaces ( $\geq 1$  ha) and the presence of green courtyards also increased nest survival.

If highly urbanized areas are not associated with a breeding advantage, why are they occupied ahead of more productive sites at the edge of the city? It is possible that there are simply too few breeding cavities in the outskirts of the city. We found nest site cavities exclusively in the center and conclude that closed breeding cavities are chosen because of their attractiveness and not because of the limited numbers of other potential types of nest, such as crow nests and window boxes. Attributes of breeding cavities such as limited accessibility to predators, protection from rain and sun, and a low probability of collapse have been associated with higher breeding success.<sup>53,54</sup> Our study appears to show the opposite, with the selection of breeding cavities in the city center associated with a lower breeding success.

## Nest failure, breeding success, and sex-biased nestling survival

Most nest failures occurred during incubation of the eggs and were connected to nest desertion or predation (Table 5). Our results do not indicate a lower rate of nest predation for urban-breeding birds, as has been documented in other studies such as in Tella, *et al.*<sup>55</sup> or Stracey<sup>56</sup> but see Evans, *et al.*<sup>57</sup> reporting higher nest predation by corvids in urban areas). Abandonment occurred during the egg stage (once after hatching) and might have related to territorial disputes or to higher ectoparasite burdens in breeding cavities.

In common with many other raptors, the kestrel shows a size dimorphism, with females larger than males.<sup>58</sup> When individuals of one sex are more costly than the other to produce, sex ratios may differ from 1:1.<sup>59</sup> A higher mortality of the more expensive sex results in an excess of the cheaper sex at fledging, and several

TABLE 5. Number of nest attempts, reproductive outcome and cause of complete nest failure for *Falco tinnunculus* in Vienna, Austria, 2010–2012

		REPRODUCTIVE OUTCOME		TIME OF NEST FAILURE		CAUSE OF NEST FAILURE		
YEAR	NEST ATTEMPTS	SUCCESS (%)	FAILURE (%)	EGG STAGE	NESTLING STAGE	ABANDONED	PREDATION <sup>#</sup>	OTHER
2010	36	21 (58%)	15 (42%)	11	4	5	4	6
2011	52	36 (69%)	16 (31%)	14	2	4	6	6
2012	69	48 (70%)	21 (30%)	18	3	6	4	11
ΤΟΤΑ	L 157	105 (67%)	52 (33%)	43	9	15	14	23

Note: "#" based on confirmed predation. If the predation event was not directly observed and the predator not identified, nest failure is assigned to other.

species of raptor are known to manipulate the sex ratio of their offspring in response to a range of factors (e.g. Anderson,<sup>60</sup> Ingraldi, *et al.*,<sup>61</sup> and Wu,<sup>62</sup> including variation in the availability of resources.<sup>63,64</sup> Kestrels have been reported to switch the sex-bias from male-dominated in early nests to female-dominated in later nests.<sup>65</sup> We found that the smaller males and the last chicks to hatch were most likely to die as nestlings. The results are consistent with the finding that kestrels breeding in the center of Warsaw had more female offspring.<sup>66</sup> The mortality of nestling Montagu's harriers (*Circus pygargus*) has also been shown to be biased, with smaller males most likely to die, especially if they hatch later in the season.<sup>67</sup> Our results do not necessarily imply a manipulation of the sex ratio but could relate simply to a greater susceptibility of the smaller (male) chicks when food resources are scarce.

#### Prey availability and diet choice

Rodents provide a higher nutritional value than avian prey.<sup>68,69</sup> Our survey of small mammals suggests that rodents are abundant in the city center and the outskirts of Vienna, but most species are nocturnal and, thus, hardly accessible to a diurnal raptor. Unlike the lesser kestrel F. naumanni, which is known to hunt during the night under artificial lighting,<sup>70</sup> the kestrel is a largely diurnal hunter. Urban kestrels thus have to fly longer distances of at least several kilometers to hunt for their preferred prey.<sup>71,72</sup> In the center of larger cities, it may be energetically preferable to switch to less profitable but more common avian prey.<sup>73</sup> Indeed, recent studies indicate that kestrel populations in some larger European cities are increasingly feeding on birds, <sup>23,34,74</sup> whereas kestrels in smaller or medium-sized European cities rely largely on a diet of voles (*Microtus* sp.), as do their rural conspecifics.<sup>24,25,72</sup> In general, kestrels are believed to feed on what is locally abundant, although there have been reports of consistent differences in diet composition between neighboring breeding pairs, presumably reflecting individual preferences for prey or differing abilities at catching different prey types.75

The increased proportion of non-rodent prey in kestrel pellets from the center of Vienna compared with those from nearer the edge of the city is evidence that the birds generally hunt in the surroundings of their nest sites. Consistent with this idea, a trade-off between the ready availability of breeding cavities and the greater distances to hunting grounds, which result in a shift in the main prey taken and a lower breeding success.

nest sites are often located close to

green courtyards. A comparative study on generalist and specialist avian predators under fluctuating food conditions has shown that a vole specialist (pallid harrier *Circus macrourus*) forages less efficiently in poor vole years because the species is less efficient at capturing alternative prey, such as birds.<sup>76</sup> The increased effort required to hunt

non-rodent prey may affect the

breeding success of kestrels in the center of Vienna. Our data indicate

#### Are inner-city buildings ecological traps for an urban raptor?

The kestrel is not truly an urban species. Although it has a strong preference for breeding in cavities, it does not profit from other human resources, nor does it show a higher degree of sociality and sedentariness.<sup>77</sup> It clearly exploits the urban environment, but high breeding densities in human-dominated landscapes do not necessarily indicate that the species benefits in terms of breeding success. Our findings are consistent with a trade-off between the availability of building cavities, which offer nest sites that are protected from potential predators, and the poorer food supply in the city center. The consequence is that kestrels appear to select nest sites that are associated with increased reproductive failure and smaller fledged broods.

It may be difficult for kestrels to evaluate food availability when they are prospecting for nest sites (Hollander, *et al.*<sup>78</sup> and Török, *et al.*<sup>79</sup> and citations therein), and errors could cause birds to overestimate the quality of the habitat<sup>78,80</sup> and settle in poor habitats despite the availability of better options. The preference for poorer habitats is a maladaptive behavior associated with socalled ecological traps (reviewed in other studies: Schlaepfer, *et al.*,<sup>19</sup> Kokko, *et al.*,<sup>43</sup> Robertson, *et al.*,<sup>46</sup> Battin,<sup>47</sup> and Kristan<sup>81</sup>). The idea that kestrels are falling into an ecological trap should be further investigated as it could be of conservation concern and might have important consequences for the viability of certain populations.

#### Conclusions

In the center of Vienna, Austria, kestrels frequently breed in roof openings in historical buildings, a structural feature that is not available in the outskirts of the city. A comparison along the urban gradient shows the smallest nearest neighbor distances for pairs that breed in the city center. The kestrel's favored prey is rodents, but in the center rodents are less abundant and largely nocturnal and thus not available to diurnally hunting raptors. Kestrels breeding in the center of Vienna consume more birds, including pigeons, and fewer rodents than kestrels in the outskirts. The city-dwelling raptor pays a high price for life in the city, with a lower reproductive success than birds breeding in the outskirts. The kestrel might appear to be an urban exploiter but, given the poor reproductive performance of urban kestrels, it is likely that the species is falling into an ecological trap. Although the kestrel is not itself of conservation concern, our findings suggest that other city-dwelling species may be faring less well than their abundance in the urban environment would appear to indicate.

#### Methods

#### Study system

The Eurasian kestrel, hereafter simply referred to as the kestrel, is the most abundant raptor in Vienna, Austria (48°12'N, 16°22'E; 415 km<sup>2</sup>, ca. 150–500m a. s. l., 1.8 million inhabitants). The estimated population density of 60–96 breeding pairs per 100 km<sup>2</sup> (see Wichmann, *et al.*<sup>32</sup>) is high compared to that in other European metropolises (e.g., see Kupko, *et al.*,<sup>82</sup> and Malher, *et al.*<sup>83</sup>) and in rural eastern Austria.<sup>84</sup> Kestrels return to Vienna at the end of March, before pair formation, and remain at their breeding sites until late summer (personal observation, PS and AG). The study period covered three breeding seasons from March 2010 to August 2012.

The river Danube, lined with riparian forest, divides Vienna in two, making distance from the city center misleading in terms of defining an urban gradient. We thus define urbanization by the percentage of sealed soil (calculated in ArcGIS 10 by ESRI,<sup>©</sup> based on land covered by buildings or areas used by traffic on a land allocation map, digitized in 55 categories of land utilization between 2007 and 2010, in a circle of radius 500 m around the nest sites; sensu<sup>85</sup>). Areas with < 1% of unsealed soil were defined as rural and excluded from the analysis. Excluding these surroundings, mostly forested and agricultural areas, the urban study area covered 243 km<sup>2</sup> (Fig. 1). Nests were distributed between percentages of sealed soil of 18% (most suburban) and 89% (most urban). By extending our search up to 1% soil sealing, we made sure that NNDs were accurate.

With the help of local media, we called on the public to report kestrel nests in Vienna in 2010 and 2011. Additionally, 25 volunteer ornithologists and PS and AG systematically searched the city for nests. Historic nest sites recorded in the BirdLife Austria archive (N= 103), occupied nests found during systematic searches (N = 124), locations of kestrel foundlings in the database of the animal shelter and the bird clinic at the University of Veterinary Medicine, Vienna (N = 78) and nest sites reported by the general public were confirmed through personal observations during pair formation and courtship and classified as occupied if adults were present on two consecutive visits. During the study period, we built a data base of 451 recent nest sites, between 50% and 65% of which were occupied each year.

#### Nest site and habitat parameters

Two different spatial levels were used to define nest site and habi-

tat parameters. The percentage of sealed soil was calculated in a circle of r = 500 m around the nest site (78.5 ha) and expressed as the percentage of land covered by buildings or areas used by traffic. The resulting value is termed the urban gradient. The distance (in m) from the nest site to the nearest open green space was recorded. The size of the nearest open green space, which was either a green courtyard or a park area in the city center or a lawn (usually in a garden), a meadow or agricultural land in the suburbs, was assigned to one of four categories,  $\geq 1$ ha,  $\geq 0.5$  ha,  $\geq 0.25$  ha and  $\geq 100$  m<sup>2</sup>.

We also described the building on which the nest was located, recording the nest height (m), façade structure, presence of roof openings or other cavities, and presence of green courtyards (between 0.01 and 0.1 ha). We counted the stick nests of crows on the façade and in surrounding trees, as well as the number of window boxes on balconies. The same parameters were measured for 240 buildings chosen at random by placing a 500×500 m grid over the study area and using each intersection that touched a building. We used the height of the attic as hypothetical "nest height" variable (as 62% of actual nest sites were located at attic level).

Habitat data were obtained via a land allocation map (1:7,500, resolution 15 cm), digitized based on geo-referenced aerial images provided by the Environmental Protection Bureau of Vienna (MA22-709/2010). Data on building structure were acquired on site.

#### **Breeding parameters**

Occupied nests that were accessible via the attic or by climbing were monitored 4-6 times during each breeding season to determine (1) the laying date, (2) the clutch size, (3) the number of hatched offspring, and (4) the number of fledged young. In total, 157 broods were examined (36 nest sites in 2010, 52 in 2011, and 69 in 2012). Kestrels start incubation after the second egg is laid and the date (variable "laying date") was estimated either directly or by subtracting 30 days from the estimated date of hatching.<sup>58</sup> We defined 1 April as day 1 of the breeding season and numbered all dates of nest inspection thereafter for analyzing survival (in total 118 days, see Rotella, et al.<sup>86</sup> for methodological details). We used the residuals of laying date and study year (calculated in an ANOVA with study year as predictor and laying date as predicted variable) to compare differences along the urban gradient. Additional covariates for nest survival models were percentage of sealed soil (%), age at which the nest was found, distance (m) from the closest open green space (area≥1 ha) as a potential large hunting ground, presence/absence of a green courtyard (between 0.01 and 0.1 ha) within r = 100 m from the nest site (factor variable 1/0) as a potential small hunting ground, area used by traffic (m<sup>2</sup>, in a circle of r = 100 m around the nest site) as an indicator of noise disturbance and the NND (m) to the next active kestrel nest. In two years, we additionally recorded for a larger data set (N = 200nests in 2010, and N = 185 nests in 2011) the dates kestrels arrive at their nest sites: the information was provided by ornithologists involved in the breeding bird survey and observers living in direct view of a nest site. Involving the general public allowed us to have observers at accessible nest sites (mostly across the street or "owners" of occupied window and nest boxes), who provided immediate information on hatching. In other cases, we estimated the date of hatching from clutch initiation or egg floating. We marked chicks after hatching with non-toxic ink until they were ringed.

During repeated monitoring, the nestlings were measured, weighed, and ringed (with rings from the Ringing Centre Radolfzell, Germany) when they were at least 10 days old (wing length  $\geq$ 54 mm). The lengths of the culmen, tail, wing, tarsus, claws, and feet<sup>87</sup> were measured for age determination.<sup>21</sup> We determined



clutch size, hatching, and fledging rates and size of the fledged brood (breeding success) for each nest. The hatching rate was recorded on a continuous scale from 0 (no eggs hatched) to 1 (all eggs hatched). The fledging rate was defined similarly and varied from 0 (no hatchling survived) to 1 (all hatched young successfully fledged). The final inspection took place in the last week of the nestling period (24–30 days after hatching). Nestlings fledge after 28–31 days,<sup>58</sup> so we considered pairs successful if they produced at least one 28-day-old chick. The size of the fledged brood was therefore the number of nestlings in successful nests at week 4.

Nests were defined as having failed if there was clutch loss during incubation or if all chicks died after hatching (as a result of predation, starvation, parasite infestation, or parental abandonment). We attributed the cause of failure to abandonment if the nest contained intact and cold eggs and no adults were present during two subsequent inspections over 1–2 weeks (sensu<sup>36</sup>) and to predation if predation was observed (crows robbing the nest during the day or broken eggs and marten tracks found in the breeding niche).

#### Sexing chicks

Sexing of chicks was based on the CHD system, Intron A.<sup>88</sup> We used the blastoderm or embryonic tissue from unhatched eggs, buccal swabs<sup>89</sup> for small nestlings (2–10 days), and blood

of pinned growing feathers for older nestlings (>10 days). DNA was extracted with the QIA-GEN DNeasy Blood & Tissue Kit® following the standard protocol with Proteinase K. Sex was determined based on the 2718R and 2550 F primer set<sup>90</sup> and confirmed with the Falco-specific fp102 and fp49 primers.<sup>91</sup> PCR amplification was performed in 25  $\mu$ l containing 0.5  $\mu$ l10 mM dNTP, 0.25  $\mu$ l of each forward and reverse primer (50 pmol/ $\mu$ l), 0.25  $\mu$ l Dynazyme Polymerase, and 2.5  $\mu$ l 10x reaction buffer. PCR was performed with 40 cycles of 2 min at 94°C, 20 s at 50°C, and 40 s at 72°C followed by 5 min at 72°C. PCR products were visualized on 2% agarose gels. The primary sex ratio was defined as the sex ratio in the full clutch (recorded in 2011 and 2012). The secondary sex ratio was defined as the sex ratio at fledging (recorded in all years).

#### Pellet analysis and abundance of prey

In 2010 and 2011, 637 pellets and remains of prey were collected from 37 different nest sites. We grouped the findings at nest sites according to their location along the urban gradient (sensu<sup>34</sup>), distinguishing between city center (288 pellets, N = 18 nests with 81-89% sealed soil), mixed zone (206 pellets, N = 10 nests, 51-80% sealed soil), and suburban areas (143 pellets, N = 9nests, 18-50% sealed soil). The pellets were dissected and prey remains classified as "mammals," "birds," "reptiles," or "insects." We identified prey to species level where possible with the aid of reference collections at the Museum of Natural History, Vienna. We assessed the minimum number of each category of prey per pellet (largest number of different jaws, upper or lower mandibles, skulls, or pairs of incisors in small mammals; plugged feathers in birds; pairs of mandibles, tarsi, or ovipositors in insects) and present data as their estimated biomass [g]: 18.8 g for small mammals, 22.4 g for sparrow-sized birds, 76.4 g for thrush-sized birds, 330 g for pigeons, 10 g for reptiles, 1.5 g for Orthoptera, and 0.2 g for *Coleoptera*.<sup>92,93</sup> Diet breadth (B) was calculated according to Levin's index<sup>94</sup> as  $B = 1/\Sigma p_i^2$ , where  $p_i$  is the proportion of the diet represented by prey type i. As variables were not normally distributed, nonparametric tests were used for analysis.

To assess the availability of potential avian prey in 2010, a team of 25 ornithologists monitored 25 transects (N = 9 in the city center, N = 9 in the mixed zone, and N = 7 in suburban areas) in the course of the Austrian breeding bird survey using the standard method of 5-minute point-counts in the early morning under stable weather conditions.<sup>95</sup> The ornithologists were recruited by Birdlife Austria and by PS. Each bird recorded within 50 m of the point was identified based on voice, appearance, or both. Analysis was based on prey known from pellet analysis<sup>33</sup> to be taken by kestrels. Potential prey was grouped by size (sparrow-, thrush-, and pigeon-sized). Transects were selected by PS in ArcGIS 10 based on the land allocation map and included buildings, areas used by traffic, green courtyards (between 0.01 and 0.1 ha), and parks (between 0.3 and 600 ha) in the city center and the mixed zone, and gardens and forest edges in the suburban area. Transects were chosen independently of the location of kestrel nests. They were sampled twice per year, at the beginning of the breeding season (in spring, calendar week 17–18, in April) and during the nestling period (in summer, calendar week 22–23, in June). Each transect consisted of 12–20 points at 300–500 m intervals.

The kestrel nest sites were assigned to the closest transects (max. distance 1 km, N = 2-24 nests/transect). It is logical to allocate a nest to a transect rather than to a point as two or more count points could be within the hunting grounds of a single pair of kestrels. Furthermore, the assignment takes into account the spatial autocorrelation of neighboring counting points on a transect. The proportion of successful breeding attempts was calculated for each transect and the figures were used to relate breeding success to availability of prey.

Densities of rodents were estimated by means of the "minimum number alive method."<sup>96</sup> We used 97 Rödl-type live traps<sup>97</sup> in 59 transects, with 10–20 traps in each of 23 different city parks (between 0.3 and 600 ha) across the urban gradient. The traps were checked twice per day (morning and evening) on two consecutive days per area at the start and the end of the 2010 breeding season, resulting in 2,676 trapping events (see master thesis<sup>98</sup> for details).

#### Statistical analysis

Differences in habitat between nest sites and buildings chosen at random were evaluated with a generalized linear model (GLM) with binomial error structure and a logit link function. The variables were nest height, facade structure, presence of roof openings or other cavities, and presence of green courtyards. One variable, houses with alcoves, was excluded because there were more roof openings in houses with alcoves ( $\chi^2$ -test, N= 248, df = 1, P<0.001) and the variable "roof openings" was obviously related to nest site and, thus, of higher biological significance.

To analyze the relationship between abundance of prey and breeding success, a GLM was constructed with proportion of successful nests as dependent variable and the two predictors "avian prey counted" and "rodents trapped." To calculate the proportion of successful nests, we used the number of successful and failed nests per transect together as response variable fitted to a binomial error distribution. This can be treated as a weighted regression using the individual sample sizes as weights and the logit link function to ensure linearity (see Crawley<sup>37</sup> for details).

All distance and area variables were logarithmically transformed. Analysis of the variation of breeding parameters with the urban gradient was performed by generalized linear mixed models (GLMM) with the lmer and glmer functions of the R package "Ime4," <sup>99</sup> including the nest site ID and the study year as random factors. Error distribution was chosen according to the response variable: Gaussian distribution and the identity link function for clutch date and date of arrival at the nest site; binomial distribution and the logit link function for rates of hatching and fledging (values between 0 and 1); and Poisson distribution with the log link function for the sizes of the clutch and the fledged brood.

Models including soil sealing (urban gradient), NND (nearest neighbor distance), and laying date (timing of breeding) as

explanatory variables were evaluated, as was a model including interactions between these variables. All explanatory variables were fitted to a maximal model and removed one by one, with the associated changes in the model deviance assessed by a likelihood ratio test.<sup>100</sup> After each step, we calculated the AICc (Akaike Information Criterion, corrected for small sample sizes) and defined the model with the lowest value as the final one.<sup>101</sup> Model selection and model weight is presented in Additional file 2. The proportion of deviance explained (%) for each fixed effect of the lmer models was analyzed with the "LMER Convenience Functions" package.<sup>102</sup> As this function has not yet been implemented for glmer models (Ime4 requires binomial and Poisson error distributions) we assessed estimates of variance explained using R2 values, following the method recently described by Nakagawa,<sup>103</sup> implemented in the "MuMIn" package.<sup>104</sup> Details on nest site and habitat parameters used for statistical analysis can be found in Additional file 3. To analyze nest survival, we used the "nest" model in "RMark."<sup>105,106</sup> We considered models with  $\Delta$ AIC<2.0 to represent good candidates.<sup>107</sup> All statistical analysis was performed with the software R version 3.0.1 (R Development Core Team 2013).

#### Ethical notes

The study was performed under license from the Ethics Committee of the University of Veterinary Medicine, Vienna, and the Environmental Protection Bureau of Vienna (MA 22/1263/2010/3). All sampling was conducted in strict accordance with current Austrian and EU law and followed the Weatherall Report and the guidelines for the treatment of animals in behavioral research and teaching.<sup>108</sup>

#### Availability of supporting data

Morphological data on kestrels have been provided to the Ringing Centre in Radolfzell, Germany. Data from the breeding bird survey have been made available to Birdlife Austria and the Environmental Protection Bureau of Vienna (MA22) for use in conservation measures. All supporting data are available from the authors on request.

#### Abbreviations

AICc: Akaike information criterion, corrected for small sample sizes; GLM: Generalized linear model; GLMM: Generalized linear mixed; NND: Nearest neighbor distance.

#### **Competing interests**

The authors declare that they have no competing interests.

#### Authors' contributions

The original idea and study design came from PS, AG, and HWK. PS performed the field and laboratory work; help by others is accordingly acknowledged. PS, EN, and GT analyzed the data. The manuscript was prepared by PS, EN, GT, and AG and approved by all authors.

ADDITIONAL FILE 1. Breeding parameters of Falco tinnunculus in Vienna, Austria, 2010-2012 (N = 157 nest sites in total) in three urban zones. Results are shown as mean value ± SD. We pooled those nest

sites according to their location along the urban gradient (city center with 81%-89% soil sealing, mixed zone with 51-80% soil sealing, and suburban area with 18-50% soil sealing).

	CITY CENTER	MIXED ZONE	SUBURBAN AREA						
2010 (N=36, IN TOTAL 251 OCCUPIED NES	2010 (N=36, IN TOTAL 251 OCCUPIED NESTS WITHIN THE URBAN STUDY AREA)								
LAYING DATE (FIRST EGG)	MAY 4 ± 6.3 D (APRIL 27)	MAY 3 ± 11.9 D (APRIL 15)	MAY 1 ± 17.6 D (APRIL 11)						
CLUTCH SIZE	2.52 ± 2.06	4.58 ± 1.73	5.00 ± 1.41						
HATCHED	1.74 ± 1.94	3.58 ± 1.78	4.40 ± 1.14						
FLEDGED PER BREEDING ATTEMPT	1.00 ± 1.33	1.58 ± 1.31	4.00 ± 1.22						
FLEDGED PER SUCCESSFUL PAIR	2.38 ± 0.92	2.38 ± 0.74	4.00 ± 1.22						
% SUCCESSFUL PAIRS	42.11% (N=8)	66.67% ( <i>N</i> =8)	100.00% ( <i>N</i> =5)						
2011 (N=52, IN TOTAL 297 OCCUPIED NESTS	)								
LAYING DATE (FIRST EGG)	MAY 4 ± 14.4 D (APRIL 7)	MAY 3 ± 15.1 D (APRIL 6)	APRIL 19 ± 7.2 D (APRIL 8)						
CLUTCH SIZE	3.88 ± 1.86	4.46 ± 1.48	5.75 ± 1.16						
HATCHED	2.38 ± 2.42	3.57 ± 1.89	4.25 ± 2.71						
FLEDGED PER BREEDING ATTEMPT	1.81 ± 1.94	2.61 ± 1.79	3.50 ± 2.39						
FLEDGED PER SUCCESSFUL PAIR	3.22 ± 1.39	3.32 ± 1.29	4.67 ± 1.21						
% SUCCESSFUL PAIRS	56.25% (N=9)	78.57% (N=22)	75.00% ( <i>N</i> =6)						
2012 (N=69, IN TOTAL 215 OCCUPIED NESTS	)								
LAYING DATE (FIRST EGG)	MAY 4 ± 11.3 D (APRIL 12)	MAY 4 ± 15.8 D (APRIL 5)	APRIL 24 ± 16.42 D (APRIL 4)						
CLUTCH SIZE	3.47 ± 2.45	4.42 ± 1.65	5.00 ± 0.93						
HATCHED	2.83 ± 2.21	3.58 ± 2.11	4.13 ± 1.88						
FLEDGED PER BREEDING ATTEMPT	2.48 ± 1.95	2.81 ± 1.99	3.53 ± 2.10						
FLEDGED PER SUCCESSFUL PAIR	3.80 ± 1.21	3.95 ± 0.95	4.42 ± 1.16						
% SUCCESSFUL PAIRS	65.22% ( <i>N</i> =15)	70.97% ( <i>N</i> =22)	80.00% ( <i>N</i> =12)						

#### Acknowledgments

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#### Additional files 1-3

See pages 26-28.

#### **Literature Cited**

- 1. Ramalho CE, Hobbs RJ. Time for a change: dynamic urban ecology. *Trends in Ecology and Evolution*. 2012; 27:179–188.
- 2. Marzluff JM. Worldwide urbanization and its effects on birds. *In:* Avian ecology and conservation in an urbanizing

ADDITIONAL FILE 2. MODEL SELECTION FOR TABLE 3 IN RESULTS SECTION (DEPENDENCE OF BREEDING PARAMETERS ON URBANIZATION). Models are ranked according to the Akaike Information Criterion, corrected for small sample sizes (AICc). The  $\Delta$ AICc indicates AICc differences between a particular model and the best-fitting model with the smallest AICc. Akaike weights ( $\omega$ i) indicate the contribution of each model to the average of all candidate models and K the number of parameters. Variables included in and excluded from a particular model are indicated by 1s and 0s, respectively. Id–laying date, ss–sealed soil, NND–nearest neighbor distance. *Good candidate models are printed in bold*.

CLUTCH SIZE     LD‡     NND†     S5     K     AICC     ΔAICC     ΩI       FINAL MODEL     1     0     1     5     516.00     0     0.40       1     1     0     1     5     518.10     2.02     0.24       1     1     1     6     518.90     2.95     0.09       0     0     0     3     520.00     4.08     0.05       0     0     1     4     520.30     4.34     0.05       0     1     0     4     522.10     6.15     0.02       FULL MODEL     0     1     1     5     187.00     0     0.61       1     1     1     5     187.00     0     0.22     0.22       1     0     1     4     190.40     3.41     0.11       1     1     0     1     4     190.40     3.41     0.11       1     1     0     1     5	TABLE 3	VARIA	ABLES INCI	LUDED	MODE	L SELECTION	BASED ON	N AICc
FINAL MODEL   1   0   0   4   516.00   0   0.40     1   0   1   5   517.00   1.02   0.24     1   1   0   5   518.10   2.10   0.14     1   1   1   6   518.90   2.95   0.09     0   0   0   3   520.00   4.08   0.05     0   0   1   4   520.30   4.34   0.05     0   1   0   4   522.00   4.04   0.02     FULL MODEL   0   1   1   5   187.00   0   6.16     FINAL MODEL   1   0   1   5   187.00   0   0.22     1   1   1   1   6   189.10   2.05   0.22     1   1   1   1   6   189.10   2.05   0.22     1   1   1   1   1   1   1   0   0   1.24   0.12     1   1   1   1	CLUTCH SIZE	LD‡	NND†	SS	К	AICc	ΔAICc	ΩI
1     0     1     5     517.00     1.02     0.24       1     1     0     5     518.10     2.10     0.14       1     1     1     6     518.90     2.95     0.09       0     0     0     3     520.00     4.08     0.05       0     0     1     4     522.30     4.34     0.05       FULL MODEL     0     1     1     4     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       1     0     1     5     192.50     5.49     0.04       1     1     0     4     190.40     3.41     0.11       1     1     0     4     194.20     7.22     0.02       1     1     1     5     196.30     9.25     0.01       FULL MODEL     1     0     1     5     196.30     9.23     0.02 <td>FINAL MODEL</td> <td>1</td> <td>0</td> <td>0</td> <td>4</td> <td>516.00</td> <td>0</td> <td>0.40</td>	FINAL MODEL	1	0	0	4	516.00	0	0.40
1     1     0     5     518.10     2.10     0.14       1     1     1     6     518.90     2.95     0.09       0     0     0     3     520.00     4.08     0.05       0     0     1     4     522.30     4.34     0.05       FULL MODEL     0     1     0     4     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICC     ΔAICC     ΩI       1     0     1     5     192.50     5.49     0.04       1     1     0     5     192.50     5.49     0.04       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       1     1     1     5     196.30     9.25     0.01       FULL MODEL     1     0     1     5     194.60     1.01     0.23 <td></td> <td>1</td> <td>0</td> <td>1</td> <td>5</td> <td>517.00</td> <td>1.02</td> <td>0.24</td>		1	0	1	5	517.00	1.02	0.24
1     1     1     6     518.90     2.95     0.09       0     0     0     3     520.00     4.08     0.05       0     0     1     4     520.30     4.34     0.05       FULL MODEL     0     1     0     4     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICC     ΔAICC     0.061       1     1     0     1     5     187.00     0     0.661       FINAL MODEL     1     0     1     5     192.50     5.49     0.04       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       FULL MODEL     0     1     0     4     100     0     2.27       FULL MODEL     1     0     1     5		1	1	0	5	518.10	2.10	0.14
0     0     0     3     520.00     4.08     0.05       0     0     1     4     520.30     4.34     0.05       FULL MODEL     0     1     0     4     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICC     ΔAICC     Ω1       FINAL MODEL     1     0     1     5     187.00     0     0.61       1     1     1     6     189.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     195.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     5     117.20     0     0.27       FULL MODEL     1     0     1     5     117.20     0     0.27       FULL MODEL     1     0     1     5     117.60 </td <td></td> <td>1</td> <td>1</td> <td>1</td> <td>6</td> <td>518.90</td> <td>2.95</td> <td>0.09</td>		1	1	1	6	518.90	2.95	0.09
0     0     1     4     520.30     4.34     0.05       0     1     0     4     522.10     6.15     0.02       FULL MODEL     0     1     1     5     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICC     ΔAICC     ΩI       FINAL MODEL     1     0     1     5     187.00     0     0.61       1     1     1     6     199.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       FULL MODEL     0     1     5     4.10     0     2.24     0.02       FULL MODEL     1     0     1     5     117.20		0	0	0	3	520.00	4.08	0.05
0     1     0     4     522.10     6.15     0.02       FULL MODEL     0     1     1     5     522.40     6.46     0.02       HATCHING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     187.00     0     0.61       1     1     1     6     189.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       FULL MODEL     0     1     5     4     20.80     13.76     0       FULL MODEL     1     0     1     5     AICc     ΔAICc     ΩIC       FINAL MODEL     1     0     1     5 <td></td> <td>0</td> <td>0</td> <td>1</td> <td>4</td> <td>520.30</td> <td>4.34</td> <td>0.05</td>		0	0	1	4	520.30	4.34	0.05
FULL MODEL     0     1     1     5     522.40     6.46     0.02       HATCHING RATE     LD#     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     187.00     0     0.61       1     1     1     6     189.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     5     HICC     ΔAICC     ΩIC       FINAL MODEL     1     0     1     5     117.20     0     0.23       INAL     0     1     1     1     1		0	1	0	4	522.10	6.15	0.02
HATCHING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     187.00     0     0.61       1     1     1     6     189.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       FULL MODEL     0     1     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0     0.23       FINAL MODEL     1     0     1     5     117.20     0     0.23       I     1     1     1     6     118.80     1.63     0.12       I     1     1	FULL MODEL	0	1	1	5	522.40	6.46	0.02
FINAL MODEL   1   0   1   5   187.00   0   0.61     1   1   1   6   189.10   2.05   0.22     1   0   0   4   190.40   3.41   0.11     1   1   0   5   192.50   5.49   0.04     0   0   1   4   194.20   7.22   0.02     0   1   1   5   196.30   9.25   0.01     0   0   0   3   199.50   12.44   0     FULL MODEL   0   1   0   4   200.80   13.76   0     FILEDGING RATE   LD‡   NND†   SS   K   AICc   ΔAICc   ΩI     FINAL MODEL   1   0   1   5   117.20   0   0.23     I   0   0   1   4   118.60   1.40   0.14     I   1   1   6   118.80   1.63   0.12     I   1   1   5   120.50   3.30	HATCHING RATE	LD‡	NND†	SS	К	AICc	ΔAICc	ΩΙ
1     1     1     6     189.10     2.05     0.22       1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FULL MODEL     1     0     1     5     117.20     0     0.27       FIAAL MODEL     1     0     1     5     117.20     0     0.23       1     0     0     4     117.60     0.38     0.23       1     1     1     6     118.80     1.63     0.12       1     1     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     1     5     628.80     0	FINAL MODEL	1	0	1	5	187.00	0	0.61
1     0     0     4     190.40     3.41     0.11       1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NNDt     SS     K     AICc     ΔAICc     ΩI       1     0     1     5     117.20     0     0.27       1     0     0     4     117.60     0.38     0.23       0     0     1     4     118.60     1.40     0.14       1     1     1     6     118.80     1.63     0.12       1     1     1     0     5     120.50     3.30     0.05		1	1	1	6	189.10	2.05	0.22
1     1     0     5     192.50     5.49     0.04       0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.23       1     0     0     4     116.60     1.40     0.14       1     1     1     6     18.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     5     528.80     0     0.47 <td></td> <td>1</td> <td>0</td> <td>0</td> <td>4</td> <td>190.40</td> <td>3.41</td> <td>0.11</td>		1	0	0	4	190.40	3.41	0.11
0     0     1     4     194.20     7.22     0.02       0     1     1     5     196.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.23       FINAL MODEL     1     0     1     4     118.60     1.40     0.14       1     0     0     1     4     118.60     1.63     0.12       1     1     1     6     118.80     1.63     0.12       1     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FINAL MODEL     1     0     1<		1	1	0	5	192.50	5.49	0.04
0     1     1     5     196.30     9.25     0.01       0     0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.27       1     0     0     4     117.60     0.38     0.23       0     0     1     4     118.60     1.40     0.14       1     1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       0     1     1     0     4     121.70     4.49     0.03       FULL MODEL     1     0     1     5     628.80 <t< td=""><td></td><td>0</td><td>0</td><td>1</td><td>4</td><td>194.20</td><td>7.22</td><td>0.02</td></t<>		0	0	1	4	194.20	7.22	0.02
0     0     3     199.50     12.44     0       FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.27       1     0     0     4     117.60     0.38     0.23       0     0     1     4     118.60     1.40     0.14       1     1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.31       FINAL MODEL     1     0     1     5     628.80     0     0.41       FINAL MODEL     1     0     5     633.70		0	1	1	5	196.30	9.25	0.01
FULL MODEL     0     1     0     4     200.80     13.76     0       FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.27       1     0     0     4     117.60     0.38     0.23       0     0     1     4     118.60     1.40     0.14       1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       0     1     1     0     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FINAL MODEL     1     0     1     5     628.80     0     0.47       1     1     1     5     633.70		0	0	0	3	199.50	12.44	0
FLEDGING RATE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     117.20     0     0.27       1     0     0     4     117.60     0.38     0.23       0     0     1     4     118.60     1.40     0.14       1     1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       1     1     0     5     120.50     3.30     0.05       FULL MODEL     0     1     1     5     628.80     0     0.47       FINAL MODEL     1     0     1     5     633.70     4.49     0.04       1     1     0     5     633.70     4.97     0.44       1     1     0     5     649.40     20.69	FULL MODEL	0	1	0	4	200.80	13.76	0
FINAL MODEL   1   0   1   5   117.20   0   0.27     1   0   0   4   117.60   0.38   0.23     0   0   1   4   118.60   1.40   0.14     1   1   1   6   118.80   1.63   0.12     0   0   0   3   119.50   2.35   0.08     1   1   0   5   119.60   2.46   0.08     1   1   0   5   120.50   3.30   0.05     FULL MODEL   0   1   0   4   121.70   4.49   0.03     FLEDGED BROOD SIZE   LD‡   NND†   SS   K   AICc   ΔAICc   ΩI     FINAL MODEL   1   0   1   5   628.80   0   0.47     1   0   0   4   632.20   3.46   0.08     1   1   0   5   633.70   4.97   0.04     0   0   1   4   647.90   1.4   0	FLEDGING RATE	LD‡	NND†	SS	К	AICc	ΔAICc	ΩI
1004117.600.380.230014118.601.400.141116118.801.630.120003119.502.350.081105119.602.460.080115120.503.300.05FULL MODEL0104121.704.490.03FLEDGED BROOD SIZELD‡NND†SSKAICcΔAICcΩIFINAL MODEL1015628.8000.471103633.704.970.041105633.704.970.040014647.9019.1400015649.4020.690003654.0025.210FULL MODEL0104656.1027.310	FINAL MODEL	1	0	1	5	117.20	0	0.27
0     0     1     4     118.60     1.40     0.14       1     1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       0     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       1     1     1     6     629.00     0.25     0.41       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     0     1     5     649.40     20.69     0 <td></td> <td>1</td> <td>0</td> <td>0</td> <td>4</td> <td>117.60</td> <td>0.38</td> <td>0.23</td>		1	0	0	4	117.60	0.38	0.23
1     1     6     118.80     1.63     0.12       0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       0     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       1     0     1     5     628.80     0     0.47       1     1     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     0     1     5     654.00     25.21     0 <td< td=""><td></td><td>0</td><td>0</td><td>1</td><td>4</td><td>118.60</td><td>1.40</td><td>0.14</td></td<>		0	0	1	4	118.60	1.40	0.14
0     0     0     3     119.50     2.35     0.08       1     1     0     5     119.60     2.46     0.08       0     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       1     1     1     6     629.00     0.25     0.41       1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     0     1     5     649.40     20.69     0       0     0     1     0     3     654.00     25.21 <t< td=""><td></td><td>1</td><td>1</td><td>1</td><td>6</td><td>118.80</td><td>1.63</td><td>0.12</td></t<>		1	1	1	6	118.80	1.63	0.12
1     1     0     5     119.60     2.46     0.08       0     1     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       I     0     1     5     628.80     0.25     0.41       I     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     0     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31		0	0	0	3	119.50	2.35	0.08
0     1     5     120.50     3.30     0.05       FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       FINAL MODEL     1     0     1     5     628.80     0     0.47       I     0     1     6     629.00     0.25     0.41       1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     0     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31 </td <td></td> <td>1</td> <td>1</td> <td>0</td> <td>5</td> <td>119.60</td> <td>2.46</td> <td>0.08</td>		1	1	0	5	119.60	2.46	0.08
FULL MODEL     0     1     0     4     121.70     4.49     0.03       FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       I     1     1     6     629.00     0.25     0.41       I     1     0     0     4     632.20     3.46     0.08       I     0     0     4     632.20     3.46     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		0	1	1	5	120.50	3.30	0.05
FLEDGED BROOD SIZE     LD‡     NND†     SS     K     AICc     ΔAICc     ΩI       FINAL MODEL     1     0     1     5     628.80     0     0.47       1     1     1     6     629.00     0.25     0.41       1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0	FULL MODEL	0	1	0	4	121.70	4.49	0.03
FINAL MODEL     1     0     1     5     628.80     0     0.47       1     1     1     6     629.00     0.25     0.41       1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0	FLEDGED BROOD SIZE	LD‡	NND†	SS	К	AICc	ΔAICc	ΩI
1     1     6     629.00     0.25     0.41       1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0	FINAL MODEL	1	0	1	5	628.80	0	0.47
1     0     0     4     632.20     3.46     0.08       1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		1	1	1	6	629.00	0.25	0.41
1     1     0     5     633.70     4.97     0.04       0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		1	0	0	4	632.20	3.46	0.08
0     0     1     4     647.90     19.14     0       0     1     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		1	1	0	5	633.70	4.97	0.04
0     1     5     649.40     20.69     0       0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		0	0	1	4	647.90	19.14	0
0     0     0     3     654.00     25.21     0       FULL MODEL     0     1     0     4     656.10     27.31     0		0	1	1	5	649.40	20.69	0
FULL MODEL 0 1 0 4 656.10 27.31 0		0	0	0	3	654.00	25.21	0
	FULL MODEL	0	1	0	4	656.10	27.31	0

Note: "‡" data presented as residuals with the study year, "†" log transformed.

world. Marzluff JM, Bowman R, Donnelly R., editors. Boston (MA): Kluwer Academic Publishers; 2001. p. 19–48.

- Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, *et al.* Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation* 2012;145:179–184.
- McKinney ML. Urbanization as a major cause of biotic homogenization. *Biological Conservation*. 2006;127:247–260.
- Rensburg BJ, Peacock DS, Robertson MP. Biotic homogenization and alien bird species along an urban gradient in South Africa. *Landscape and Urban Planning*. 2009;92:233–241.
- Miller JR, Hobbs RJ. Conservation where people live and work. *Conser*vation Biology. 2002;16:330–337.
- 7. McDonald RI, Kareiva P, Forman RTT. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation.* 2008;141:1695–1703.
- Slabbekoorn H, Ripmeester EAP. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*. 2008;17:72–83.
- Zhou D, Chu L. How would size, age, human disturbance, and vegetation structure affect bird communities of urban parks in different seasons? *Journal of Ornithology*. 2012;153:1101–1112.
- Nemeth E, Brumm H. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour.* 2009;78:637–641.
- Dominoni D, Goymann W, Helm B, Partecke J. Urban-like night illumination reduces melatonin release in European blackbirds (*Turdus merula*): implications of city life for biological time-keeping of songbirds. *Frontiers in Zoology*. 2013;10:60.
- 12. Chamberlain DE, Cannon AR,

#### ADDITIONAL FILE 3. Nest site and habitat parameters used for statistical analysis.

Habitat parameters	Detailed description	Nest site parameters	Detailed description
Urban gradient	percentage of sealed soil (%), based on land covered by buildings or areas used by traffic calculated on a land allocation map (1:7,500, resolution 15 cm) digitized in E5 setenceing of land	Height	m, height of the nest site or height of the attic as hypothetical 'nest height' variable (as 62% of actual nest sites were located at attic level)
	utilization between 2007 and 2010, in a circle of radius 500 m around the nest sites and random points.	Facade structure	presence/absence of stucco work
		Roof openings	presence/absence of specific architech- tural element (generally on buildings dating from pre-1940, especially from the so-called 'Gründerzeit' between 1848 and 1873) in the historic districts of Vienna, located between the high est row of windows and the roof; 24- 62 cm in width, 16-50 cm in depth and 24-48 cm in height
			- 2º -
Mixed zone	51-80% sealed soil		at a the
Suburban area	18-50% sealed soil		- Laka-
NND	m, nearest neighbor distance to the closest active kestrel nest	Other building cavities	presence/absence_matching the size
Distance to nearest open green space	m, assigned to four different size categories, $\ge 1$ ha, $\ge 0.5$ ha, $\ge 0.25$ ha, $\ge 100$ m2		of a suitable breeding cavity
Traffic area	affic area m2, measured in a circle of radius 100m around the nest site as an indi- cator for noise disturbance		
		Green courtyard	presence/absence, size between 0.01 and 0.1 ha

Toms MP, Leech DI, Hatchwell BJ, *et al.* Avian productivity in urban landscapes: a review and meta-analysis. *Ibis.* 2009;151:1–18.

- Shanahan DF, Strohbach MW, Warren PS, Fuller RA. The challenges of urban living. *In:* Avian urban ecology behavioural and physiological adaptations. Gil D, Brumm H, editors. Oxford University Press: Oxford (UK); 2014. p. 3–20.
- Møller AP, Diaz M, Flensted-Jensen E, Grim T, Ibáñez-Álamo J, *et al.* High urban population density of birds reflects their timing of urbanization. *Oecologia*. 2012;170:867–875.
- Møller AP. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*. 2009;159:849–858.
- 16. Blair RB. Land use and avian species diversity along an urban gradient. *Ecological Applications*. 1996;6:506–519.
- 17. González-Oreja JA. Birds of different biogeographic origins respond in contrasting ways to urbanization. Biological Conservation. 2011;144:234–242.
- 18. Chace JF, Walsh JJ. Urban effects on native avifauna: a review. *Landscape and Urban Planning*. 2006;74:46–69.
- Schlaepfer MA, Runge MC, Sherman PW. Ecological and evolutionary traps. *Trends in Ecological Evolution*. 2002;17:474–480.
- 20. Cramp S, Tomlins AD. The birds of inner London 1951–65. *British Birds*. 1966;59:209–233.
- 21. Kostrzewa R, Kostrzewa A. Der turmfalke: überlebensstrategien eines greifvogels (The kestrel: survival strategies of a raptor species). Wiesbaden: Aula Verlag; 1993.
- 22. Darolová A. Nesting of *Falco tinnunculus* (Linnaeus, 1758) in the urban agglomeration of Bratislava. *Biologia* (Bratislava). 1992;47:389–397.
- 23. Piattella A, Salvati L, Manganaro A, Fattorini S. Spatial and temporal variations in the diet of the common kestrel (*Falco tinnunculus*) in Rome, Italy. *Journal of Raptor Research*. 1999;33:172–175.
- 24. Rejt L. Peregrine falcon and kestrel in urban environment the case of Warsaw. *In:* Naturschutz und Verhalten. Volume 2/2001. Gottschalk E, Barkow A, Mühlenberg M, Settele J, editors. *Frontiers in Zoology*. 2001;81–85.
- 25. Romanowski J. On the diet of urban kestrels (*Falco tin-nunculus*) in Warsaw. *Buteo.* 1996;8:123–130.
- 26. Salvati L, Manganaro A, Fattorini S, Piattella E. Population features of kestrels *Falco tinnunculus* in urban, suburban, and rural areas in central Italy. *Acta Ornitholigica*. 1999;34:53–58.
- 27. Sommani E. Note sulla biologia di alcune coppie di Gheppio, *Falco tinnunculus*, presenti in Roma [Notes on the biology of some pairs of kestrels, *Falco tinnunculus*, in Rome]. *Riv Ital Orn Milano*. 1986;56:40–52.
- 28. Garaffa PI, Filloy J, Bellocq MI. Bird community responses along urban–rural gradients: Does the size of the urbanized

area matter? *Landscape and Urban Planning*. 2009;90:33–41.

- 29. Sorace A, Gustin M. Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning*. 2009;90:111–118.
- Lerman SB, Warren PS, Gan H, Shochat E. Linking foraging decisions to residential yard bird composition. *PLoS ONE*. 2012;7:e43497.
- 31. Pellissier V, Cohen M, Boulay A, Clergeau P. Birds are also sensitive to landscape composition and configuration within the city centre. *Landscape and Urban Planning*. 2012;104:181–188.
- 32. Wichmann G, Dvorak M, Teufelbauer N, Berg H-M. *In:* Die Vogelwelt Wiens Atlas der Brutvögel. (The avifauna of Vienna: atlas of breeding birds). Wien: Verlag Naturhistorisches Museum Wien; 2009.
- 33. Sumasgutner P, Krenn HW, Düesberg J, Gaspar T, Gamauf A. Diet specialisation and breeding success along an urban gradient: the kestrel (*Falco tinnunculus*) in Vienna, Austria. *Beiträge Zur Jagd und Wildforschung*. 2013;38:385–397.
- 34. Kübler S, Kupko S, Zeller U. The kestrel (*Falco tinnunculus*) in Berlin: investigation of breeding biology and feeding ecology. *Journal of Ornithology*. 2005;146:271–278.
- 35. Riegert J, Fuchs R. Fidelity to roost sites and diet composition of wintering male urban common kestrels *Falco tinnunculus. Acta Ornithologica.* 2011;46:183–189.
- 36. Strasser EH, Heath JA. Reproductive failure of a humantolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*. 2013;50:912–919.
- 37. Crawley MJ. The R book. London (UK): John Wiley & Sons; 2007. Chapter 16, Proportion data; p. 569–591.
- 38. Jenrich J, Löhr P-W, Müller F. Kleinsäuger: Körper-und Schädelmerkmale. Imhof: *Ökologie*; 2010.
- 39. Spitzenberger F. Die Säugetierfauna Österreichs. Graz: Austria Medien-Service; 2001.
- 40. Mitter G, Sumasgutner P, Gamauf A. City centre or periphery? Distribution and morphological adaptation of Apodemus taxa along an urban gradient. *Beiträge Zur Jagd und Wildforschung*. 2013;38:305–319.
- 41. Newton I. Population ecology of raptors. Vermillion (SD) USA: Buteo Books; 1979. p. 55–75.
- 42. Village A. The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. *Journal of Animal Ecology.* 1983;52:635–645.
- 43. Kokko H, Sutherland WJ. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research.* 2001;3:537–551.
- 44. Hromada M, Antczak M, Valone TJ, Tryjanowski P. Settling decisions and heterospecific social information use in shrikes. *PLoS ONE*. 2008;3:e3930.
- 45. Stamps JA. The silver spoon effect and habitat selection by

natal dispersers. Ecology Letters. 2006;9:1179-1185.

- 46. Robertson BA, Hutto RL. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology.* 2006;87:1075–1085.
- 47. Battin J. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*. 2004;18:1482–1491.
- 48. Gamauf A, Tebb G, Nemeth E. Honey buzzard *Pernis apivorus* nest site selection in relation to habitat and the distribution of goshawk *Accipiter gentilis*. *Ibis*. 2013;155:258–270.
- 49. Fuller RJ. Birds and habitat: relationships in changing landscapes. New York (NY): Cambridge University Press; 2012.
- 50. Chalfoun AD, Schmidt KA. Adaptive breeding-habitat selection: Is it for the birds? *Auk.* 2012;129:589–599.
- 51. Sergio F, Blas J, Forero MG, Donzar JA, Hiraldo F. Sequential settlement and site dependence in a migratory raptor. *Behavioral Ecology.* 2007;18:811–821.
- 52. Fretwell SD. Populations in a seasonal environment. Princeton (NJ): Princeton University Press; 1972.
- 53. Charter M, Izhaki I, Bouskila A, Leshem Y, Penteriani V. The effect of different nest types on the breeding success of Eurasian kestrels (*Falco tinnunculus*) in a rural ecosystem. *Journal of Raptor Research*. 2007;41:143–149.
- López BC, Potrony D, López A, Badosa E, Bonada A, et al. Nest-box use by boreal owls (*Aegolius funereus*) in the Pyrenees mountains in Spain. *Journal of Raptor Research*. 2010;44:40–49.
- 55. Tella JL, Hiraldo F, Donazar-Sancho JA, Negro JJ. Costs and benefits of urban nesting in the lesser kestrel. *In:* Raptors in human landscapes, adaptations to built and cultivated environments. Bird DM, Varlan DE, Negro JJ, editors. New York (NY): Academic Press; 1996. p. 53–60.
- 56. Stracey CM. Resolving the urban nest predator paradox: the role of alternative foods for nest predators. *Biological Conservation*. 2011;144:1545–1552.
- 57. Evans KL, Newson SE, Gaston KJ. Habitat influences on urban avian assemblages. *Ibis.* 2009;151:19–39.
- 58. Village A. The kestrel. London (UK): T & AD Poyser; 1990.
- 59. Clutton-Brock TH. Sex ratio variation in birds. *Ibis.* 1986;128:317–329.
- Anderson DJ, Reeve J, Bird DM. Sexually dimorphic eggs, nestling growth, and sibling competition in American kestrels *Falco sparverius*. *Functional Ecology*. 1997;11:331–335.
- 61. Ingraldi MF. A skewed sex ratio in northern goshawks: is it a sign of a stressed population? *Journal of Raptor Research*. 2005;39:247.
- 62. Wu H, Wang H, Jiang Y, Lei F, Gao W. Offspring sex ratio in Eurasian kestrel *(Falco tinnunculus)* with reversed sexual size dimorphism. *Chinese Birds*. 2010;1:36–44.
- 63. Rutz C. Brood sex ratio varies with diet composition in a generalist raptor. *Biological Journal of the Linnean Society*. 2012;105:937–951.

- 64. Millon A, Bretagnolle V. Nonlinear and population-specific offspring sex ratios in relation to high variation in prey abundance. *Oikos.* 2005;108:535–543.
- 65. Dijkstra C, Daan S, Buker JB. Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology*. 1990;4:143–147.
- 66. Rejt L, Gryczynska-Siemiatkowska A, Rutkowski R, Malewska A. Does egg sex ratio in urban kestrels (*Falco tinnunculus*) differ from parity? *Polish Journal of Ecology*. 2005;53:545–552.
- 67. Arroyo B. Sex-biased nestling mortality in the Montagu's harrier *Circus pygargus. Journal of Avian Biology.* 2002;33:455–460.
- 68. Goodwin TW. The biochemistry of the carotenoids. 2nd ed. London (UK) and New York (NY) USA: Chapman and Hall; 1980.
- 69. Kirkwood JK. Energy requirements for maintenance and growth of wild mammals, birds, and reptiles in captivity. *Journal of Nutrition.* 1991;121:S29–34.
- Negro JJ, Bustamante J, Melguizo C, Ruiz JL, Grande JM. Nocturnal activity of lesser kestrels under artificial lighting conditions in Seville, Spain. *Journal of Raptor Research*. 2000;34:327–329.
- 71. Riegert J, Fainová D, Mikeš V, Fuchs R. How urban kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation? *Acta Ornithologica*. 2007;42:69–76.
- 72. Riegert J, Dufek A, Fainová D, Mikeš V, Fuchs R. Increased hunting effort buffers against vole scarcity in an urban kestrel *Falco tinnunculus* population: capsule. *In:* years with low vole abundance birds visited hunting grounds more frequently and for longer. *Bird Study.* 2007;54:353–361.
- 73. Korpimäki E. Diet of the kestrel *Falco tinnunculus* in the breeding season. *Ornis Fennica*. 1985;62:130–137.
- 74. Quere J. Approche du régime alimentaire du faucon crécerelle (*Falco tinnunculus* L., 1758) en milieu urbain (Paris intra muros) et durant la période de reproduction. (Study of the kestrel's (*Falco tinnunculus*) diet in a urban environment (Paris) during the breeding period). *Le Passer*. 1990;27:92–107.
- Costantini D, Casagrande S, Di Lieto G, Fanfani A, Dell'Omo G. Consistent differences in feeding habits between neighbouring breeding kestrels. *Behaviour*. 2005;142:1409–1421.
- 76. Terraube J, Arroyo B, Madders M, Mougeot F. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos.* 2011;120:234–244.
- 77. Kark S, Iwaniuk A, Schalimtzek A, Banker E. Living in the city: can anyone become an "urban exploiter"? *Journal of Biogeography.* 2007;34:638–651.
- 78. Hollander FA, Titeux N, Van Dyck H. Habitat-dependent prey availability and offspring provisioning explain an ecological trap in a migratory bird. *Functional Ecology.*

2013;27:702-709.

- 79. Török J, Hegyi G, Tóth L, Könczey R. Unpredictable food supply modifies costs of reproduction and hampers individual optimization. *Oecologia*. 2004;141:432–443.
- Kloskowski J. Fish stocking creates an ecological trap for an avian predator via effects on prey availability. *Oikos.* 2012;121:1567–1576.
- 81. Kristan WB. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos.* 2003;103:457–468.
- Kupko S, Schlottke L, Rinder J. Der turmfalke (*Falco tin-nunculus* L.) im Berliner stadtgebieteine auswertung unter besonderer berücksichtigung der monitoringfläche Nr. 376 (Berlin-West). *Populationsökologie Greifvogel und Eulenarten*. 2000;4:359–372.
- Malher F, Lesaffre G, Zucca M, Coatmeur J. Oiseaux nicheurs de Paris. Un atlas urbain. (The breeding birds of Paris. An urban atlas). Paris: Corif. Delachaux et Niestlé; 2010.
- 84. Gamauf A. Greifvögel in Österreich. Bestand-Bedrohung-Gesetz. (Birds of prey in Austria. Population-Threat-Law). Wien: Umweltbundesamt Wien; 1991.
- 85. Zuckerberg B, Bonter DN, Hochachka WM, Koenig WD, DeGaetano AT, *et al.* Climatic constraints on wintering bird distributions are modified by urbanization and weather. *Journal of Animal Ecology.* 2011;80:403–413.
- 86. Rotella JJ, Dinsmore SJ, Shaffer TL. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation.* 2007;27:187–205.
- 87. Eck S, Fiebig J, Fiedler W, Heynen I, Nicolai B, *et al.* Deutsche Ornithologen-Gesellschaft: vögel vermessen [DO-G: measuring birds]. Christ Media Natur; 2011.
- Griffiths R, Double MC, Orr K, Dawson RJG. A DNA test to sex most birds. *Molecular Ecology*. 1998;7:1071–1075.
- 89. Wellbrock A, Bauch C, Rozman J, Witte K. Buccal swabs as a reliable source of DNA for sexing young and adult common swifts (*Apus apus*). *Journal of Ornithology*. 2012;153:991–994.
- 90. Fridolfsson A-K, Ellegren H. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*. 1999;30:116–121.
- 91. Nesje M, Røed KH. Sex identification in falcons using microsatellite DNA markers. *Hereditas*. 2000;132:261–263.
- 92. Arroyo BE. Diet of Montagu's harrier *Circus pygargus* in central Spain: analysis of temporal and geographic variation. *Ibis.* 1997;139:664–672.
- 93. von Blotzheim UNG, Bauer KM. Handbuch der Vögel Mitteleuropas. *Columbiformes–Piciformes*. (Handbook of the birds of Central Europe, *Columbiformes-Piciformes*). Wiesbaden: Aula-Verlag; 1980. p. 232–234.
- 94. Levins R. Evolution in changing environments; some theoretical explorations. Princeton (NJ): Princeton University

Press; 1968.

- 95. Südbeck P, Andretzke H, Fischer S, Gedeon K, Schikore T, *et al.* Methodenstandards zur Erfassung der Brutvögel Deutschlands. (Methods for the detection of breeding birds in Germany). Radolfszell: Die Deutsche Bibliothek; 2005.
- 96. Krebs CJ. Population cycles revisited. *Journal of Mammalogy*. 1996;77:8–24.
- 97. Janova E, Nesvadbrova J, Heroldova M, Bryja J. Effectiveness of two trapping protocols for studying the demography of common voles. *Hystrix Italian Journal of Mammalogy*. 2010;21:189–193.
- 98. Wiener Stadtgebiet MG:Ki: Der Einfluss öffentlicher Parks und Grünanlagen auf Häufigkeit und Morphologie. (Rodents in the city of Vienna: Distribution and morphological adaptation along an urban gradient). Master thesis. Fakultät für Lebenswissenschaften: Universität Wien; 2012. p. 19–27.
- 99. Bates D, Maechler M. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-32; 2013.
- 100. Zuur AF, Ieno EE, Walker NJ, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. New York (NY): Springer; 2009. p. 220–223.
- Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*. 2011;65:23–35.
- 102. Tremblay A, Ransijn J. Package "LMER Convenience Functions"; 2013.
- 103. Nakagawa S, Schielzeth H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*. 2013;4:133–142.
- 104. Barton K. MuMIn: Multi-model inference. R package version 1.9.5; 2013.
- White GC, Burnham KP. Program MARK: survival estimation from populations of marked animals. *Bird Study*. 1999;46:S120–S139.
- 106. Laake JL, Johnson DS, Conn PB. Marked: an R package for maximum likelihood and MCMC analysis of capture-recapture data. *Methods in Ecology and Evolution*. 2013;4:885–890.
- 107. Krebs CJ. Ecological Methodology. 4th ed. Menlo Park (CA): Benjamin Cummings; 2014. p. 149–159.
- ASAB: Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*. 2012;83:301–309.

#### SELECTED ABSTRACTS

#### Emerging infectious diseases in free-ranging wildlife–Australian Zoo based wildlife hospitals contribute to national surveillance

K Cox-Witton, A Reiss, R Woods, V Grillo, RT Baker, *et al. PLoS ONE* 9(5): e95127.

Emerging infectious diseases are increasingly originating from wildlife. Many of these diseases have significant impacts on human health, domestic animal health, and biodiversity. Surveillance is the key to early detection of emerging diseases. A zoo-based wildlife disease surveillance program developed in Australia incorporates disease information from free-ranging wildlife into the existing national wildlife health information system. This program uses a collaborative approach and provides a strong model for a disease surveillance program for free-ranging wildlife that enhances the national capacity for early detection of emerging diseases.

# *Campylobacter jejuni* infections associated with raccoon contact at a wildlife rehabilitation center

S Saunders, K Smith, R Schott, J Scheftel. *Council of State and Territorial Epidemiologists Annual Conference*, June 2014.

In September 2013, the Minnesota Department of Health identified two Campylobacter jejuni cases who reported having volunteered at the same wildlife rehabilitation center (WRC). The cases' isolates were indistinguishable by pulsedfield gel electrophoresis. An investigation was initiated to determine whether there was an association between volunteering at the WRC and illness. Cases were defined as people who volunteered at the WRC during July-September 2013 and experienced fever and diarrhea, or diarrhea lasting  $\geq$ 3 days, within one week of working at the WRC. Controls were defined as individuals who had volunteered at the WRC during July-September 2013. Cases and controls were interviewed about animal species handled, tasks performed, use of personal protective equipment (PPE), disease training, eating and drinking habits at the WRC, and hand washing. Odds ratios and 95% confidence intervals were calculated using logistic regression for binomial variables. T-tests were performed for continuous variables. Pooled animal fecal samples were collected from six different animal locations: avian nursery, waterfowl nursery, laundry room, raccoon nursery, squirrel nursery, and rabbit room. Of the 184 individuals enrolled, 18 (10%) met the case definition. This was an outbreak of Campylobacter jejuni infections associated with raccoon contact among volunteers/staff at a wildlife rehabilitation center. Raccoons (Procyon lotor) were identified as the source of infection through a case-control study and through isolation of the outbreak strain of Campylobacter jejuni from raccoon feces. Increased infection control measures and regular training of personnel on zoonotic diseases were recommended, and the importance of PPE usage and hand washing were stressed.

#### Veterinary treatment and rehabilitation of indigenous wildlife

E Mullineaux. *Journal of Small Animal Practice*. 2014;55:293–300

Veterinary surgeons in general practice are frequently presented with injured or orphaned animals by wildlife rescue centers, members of the public, or police officers. Following treatment, many of these animals are released to the wild. Despite the large numbers of wildlife casualties rehabilitated in this way, there are few published data detailing species, numbers treated, quality of care provided, and outcome following release. There is also ongoing debate regarding the welfare and conservation benefits of such human intervention. This article reviews the available published evidence on wildlife rehabilitation and offers recommendations on future policy.

#### Raptor gastroenterology

M Murray. *Veterinary Clinics of North America: Exotic Animal Practice*. 2014;17(2):211–234. Free-living raptors are frequently presented

to wildlife rehabilitation centers, often due to anthropogenic factors, such as motor vehicle collisions and toxicoses. Restoring these birds to health and returning them to the wild is both challenging and rewarding. A thorough understanding of the anatomy, physiology, and natural history of these species is crucial to successful treatment and rehabilitation. This article addresses raptor gastroenterology with an emphasis on conditions affecting free-living birds.

#### Evaluation of enrofloxacin use in koalas (*Phascolarctos cinereus*) via population pharmacokinetics and Monte Carlo simulation

LA Black, CB Landersdorfer, JB Bulitta, JE Griffith, M Govendir. *Journal of Veterinary Pharmacology and Therapeutics*. 2014;37(3):301–311.

Clinically normal koalas (n = 6) received a single dose of intravenous enrofloxacin (10 mg/kg). Serial plasma samples were collected over 24 h, and enrofloxacin concentrations were determined via highperformance liquid chromatography. Population pharmacokinetic modeling was performed in S-ADAPT. The probability of target attainment (PTA) was predicted via Monte Carlo simulations (MCS) using relevant target values (30-300) based on the unbound area under the curve over 24 h divided by the minimum inhibitory concentration (MIC) (fAUC<sub>0-24</sub>/MIC), and published subcutaneous data were incorporated (Griffith et al., 2010). A two-compartment disposition model with allometrically scaled clearances (exponent: 0.75) and volumes of distribution (exponent: 1.0) adequately described the disposition of enrofloxacin. For 5.4 kg koalas (average weight), point estimates for total clearance (SE%) were 2.58 L/h (15%), central volume of distribution 0.249 L (14%), and peripheral volume 2.77 L (20%). MCS using a target  $fAUC_{0-24}/MIC$ of 40 predicted highest treatable MICs of 0.0625 mg/L for intravenous dosing and 0.0313 mg/L for subcutaneous dosing of 10 mg/kg enrofloxacin every 24 h. Thus, the frequently used dosage of 10 mg/ kg enrofloxacin every 24 h subcutaneously may be appropriate against grampositive bacteria with MICs≤0.03 mg/L (PTA>90%), but appears inadequate against gram-negative bacteria and Chlamydiae in koalas.

### Managing pet cats: a New Zealand perspective

By Dr. Yolanda van Heezik, Guest Columnist



This column—the second in a series of three exploring the impact of free-roaming cats on native wildlife—comes from Dr. Yolanda van Heezik, Senior Lecturer in the Department of Zoology at the University of Otago (New Zealand).

She'll be right" is a Kiwi idiom expressing confidence that whatever is wrong will solve itself in time. It's thought to encapsulate the laid-back optimistic attitude attributed to many New Zealanders. This approach towards cat ownership was certainly prevalent in New Zealand until about a year ago when Gareth Morgan, a philanthropist economist with a combative personality, a passion for the environment, and a very thick skin, launched the "Cats to Go" media campaign to raise awareness about the impacts of pet cats on native wildlife.

When the Gareth Morgan Foundation designed its campaign, a number of scientific studies had identified pet cats as significant predators of wildlife in New Zealand cities, but this information had not translated into any changes in policy or regulations regarding cat ownership. It took the media campaign to raise awareness of the problem and create a nationwide debate, resulting in the passage of regulations by some councils.

Cats have been introduced around the globe, but the most severe impacts have been felt on islands, including New Zealand, because they lack native terrestrial predators.<sup>1,2</sup> Cat ownership trends in New Zealand are similar to those in other countries, with a density of about 220/km<sup>2</sup> across suburban landscapes.<sup>3</sup> Pet cats are typically free-ranging, with no limitations on the number of cats owned.

Several studies in urban areas have shown cats catch significant numbers of wild birds and reptiles.<sup>4,5,3</sup> Compared to other countries, urban landscapes in New Zealand support low numbers of native woodland birds, and in one small city they made up less than 10% of the total count in high housing density suburbs and less than a third in well vegetated low density suburbs.<sup>6</sup> A number of native woodland bird species absent from the urban areas can be found in exurban habitat, although it is not clear whether the presence of cats is the primary limiting factor in cities.

While New Zealanders' attitudes about pet cats are not so different from those of people in many other countries, the absence of native mammals and a suite of introduced predators means that managing cats in New Zealand is not a simple case of applying strategies proven effective elsewhere. For example, curfews are one of the more palatable management options for cat owners and should reduce hunting pressure on small nocturnal mammals and birds. Proposed in New Zealand, curfews are less appropriate as there are few native small urban mammals. Meso-predator effects<sup>7</sup> could cause curfews to be counterproductive, since night-time predation by cats on rats (another introduced species) may suppress rat populations. Curfews could lead to a larger rat population and, subsequently, more damage to native wildlife. Unfortunately, it is difficult to set up a well-designed experiment to investigate the consequences of removing free-ranging cats from urban areas. The Gareth Morgan Foundation argues convincingly that cat control should be accompanied by rat control, although most widely used and effective methods for killing rats (e.g., poisons) are not appropriate in urban areas.

Cat owners may be likely to keep their pets inside more out of concern for the welfare of the cat than for the welfare of wildlife populations.<sup>8</sup> Cat owners who confine their cats 24/7 typically do so as protection from diseases (e.g., rabies) and encounters with larger predators,<sup>9,10</sup> but there are fewer causes of concern in New Zealand as rabies and larger predators are mostly absent. In New Zealand, the role cats play as vectors of zoonotic disease has not yet received much public attention,



but public education about issues such as toxoplasmosis may provide motivation for greater control over cat numbers and movements. Duffy and Capece<sup>11</sup> suggest future health concerns about zoonotic diseases may serve as the catalyst to change public acceptance of free-ranging cats.

It's interesting that in a country where predator management is the main focus of conservation efforts to protect native biodiversity, so little attention has been directed towards domestic cats. Predator management is typically concentrated on islands, in forests, alpine areas, and across drylands. Conversely, the urban landscape, where domestic cats are the principle predator, typically lack any effective form of control.

Community-lead restoration initiatives are becoming a common conservation activity in New Zealand.<sup>12</sup> A group will identify a site of interest, then embark on a process of weed control, planting native vegetation, and predator control, often in collaboration with the Department of Conservation. Reintroduction of locally extinct birds such as kiwi (*Apteryx* spp.) and saddleback (*Philesturnus caruncula*- tus) is the goal of many such initiatives. When the causes of extinction have been removed (e.g., predators) and there is sufficient habitat to support the species, many of these attempts succeed. Wildlife restorations should take place in urban areas as well, to enable the majority of the population to encounter wildlife within their neighborhoods, but the unregulated presence of free-roaming pet cats stymies any aspirations to reintroduce species vulnerable to predation. Hopefully, the momentum created by the "Cats to Go" media campaign will result in action by councils to regulate cat ownership and manage un-owned cats. The New Zealand public is at the beginning of a process that requires us to think about how we value our native biodiversity. According to Wikipedia, the term "she'll be right" has recently gained a less flattering connotation, indicating a "willingness to accept a low-quality or makeshift situation rather than seek a more desirable solution." With any luck, that won't apply to the way we choose to protect our wildlife from cats.

#### **Literature Cited**

- Nogales M, Martin A, Tershie BR, Donlan CJ, Veitch D, *et al.* A review of feral cat eradication on islands. *Conservation Biology*. 2004;18:1–10.
- Medina FM, Bonnaud E, Vidal E, Nogales M. Underlying impacts of invasive cats on islands: not only a question of predation. *Biodiversity* and Conservation. 2014;23:327–342.
- van Heezik Y, Smyth A, Adams A, Gordon J. Do cats impose an unsustainable harvest on urban bird populations? *Biological Conservation*. 2010;143:121–130.
- Gillies C, Clout M. The prey of domestic cats (*Felis catus*) in two suburbs of Auckland City, New Zealand. *Journal of Zoology, London*. 2003;259, 309–315.
- Morgan SA, Hansen CM, Ross RG, Hickling GJ, Olgivie SC, et al. Urban cat (*Felis catus*) movements and predation activity associated with a wetland reserve in New Zealand. Wildlife Research. 2009;36:574–580.

- 6. van Heezik Y, Smyth A, Mathieu R. Diversity of native and exotic birds across an urban gradient in a New Zealand city. *Landscape and Urban Planning*. 2008a;87, 223–232.
- Courchamp F, Langlais M, Sugihara G. Cats protecting birds: modelling the meso-predator release effect. *Journal of Animal Ecology*. 1999;68:282–292.
- Farnworth MJ, Watson H, Adams, NJ. Understanding attitudes towards the control of non-native wild and feral mammals: similarities and differences in the opinions of the general public, animal protectionists, and conservationists in New Zealand (Aotearoa). *Journal* of Applied Animal Welfare Science. 2013. doi:10.1080/10888705.2013. 799414.
- Crooks KR, Soule ME. Meso-predator release and avifaunal extinctions in a fragmented system. *Nature*. 1999;400:563–566.
- Glen AS, Dickman CR, Soule ME, Mackey BG. Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Australian Ecology*. 2007;32:492–501.
- Duffy DC, Capece P. Biology and impacts of Pacific island invasive species. The domestic cat (*Felis catus*). *Pacific Science*. 2012;66:173–212.
- 12. Rush, M. From seed to success. a guide for community conservation projects. 2003. Department of Conservation Report, New Zealand.

Yolanda van Heezik is a senior lecturer at the University of Otago, in Dunedin, New Zealand. Together with a team of post-grads and colleagues, her urban-based research has examined birds and other wildlife in urban areas, impacts of cats on urban wildlife, biodiversity of private gardens, resident attitudes, motivations and knowledge about biodiversity, and cat ownership and control. Most recently, she has been engaged in a multi-disciplinary study exploring children's connection with nature in New Zealand cities.



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As he watched in astonishment, Phineas suddenly realized he should never, ever vacation in Las Vegas.

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Koala (Phascolarctos cinereus).



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