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From the Field

Illuminating the Nocturnal Habits of Owls with Emerging Tagging Technologies

CONNOR M. WOOD,[1,2] *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
CEEANNA ZULLA,[2] *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
SHEILA WHITMORE,[2] *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
DANA REID,[2] *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
H. ANU KRAMER, *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
JOHN J. KEANE, *U.S. Forest Service Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA*
SARAH C. SAWYER, *U.S. Forest Service Region 5, 1323 Club Dr, Vallejo, CA 94592, USA*
KEVIN N. ROBERTS, *Sierra Pacific Industries, PO Box 496028, Redding, CA 96049, USA*
BRIAN P. DOTTERS, *Sierra Pacific Industries, PO Box 496028, Redding, CA 96049, USA*
HOLGER KLINCK, *Cornell Lab of Ornithology, 159 Sapsucker Woods Rd, Ithaca, NY 14850, USA*
WILLIAM BERIGAN, *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
R. J. GUTIÉRREZ, *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*
M. ZACHARIAH PEERY, *University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*

ABSTRACT Owls play important cultural, ecological, and indicator roles throughout the world. Yet owls' cryptic behavior has led to uncertainties about their basic ecology, including foraging, communication, and functional roles within the community, and potentially hindered the implementation of effective conservation measures. Here we demonstrate the potential for next-generation GPS tags capable of recording high-precision, minute-by-minute locations paired with other technologies to resolve some of these uncertainties. We combined high-precision GPS tagging data with infrared (IR) video recorded by arboreally-mounted cameras at 5 spotted owl (*Strix occidentalis*) nest sites in the Sierra Nevada, USA to provide a uniquely detailed examination of owl foraging patterns. Our approach allowed us to identify the precise time and location of 54 predation events and prey identity. We also used high-precision GPS tags with on-board audio recorders to map the vocal activity of 8 individuals by matching the time of vocalizations in the audio data to GPS locations recorded at one-minute intervals. The combined spatial and acoustic data revealed that nonbreeding males had the most widespread territorial vocal activity (i.e., producing 4-note territorial calls), while females provisioning fledglings displayed extensive nonterritorial vocal activity (i.e., producing many contact calls). Thus, the GPS-tag technologies we employed can provide opportunities to better understand owl foraging, communication, territoriality, and population dynamics. The methods we describe are time- and resource-intensive but can be paired with techniques that are more applicable at landscape scales, such as stable isotope analyses, LiDAR-based habitat analyses, and passive acoustic monitoring to link local processes to broad-scale ecological patterns. Therefore, our approach could be applied to many species whose behavior inhibits direct observation.

KEY WORDS behavioral ecology, bioacoustics, communication, foraging ecology, GPS tag, infrared camera, passive acoustic monitoring, single-rope technique, *Strix occidentalis*.

Owls are a dominant nocturnal predator in many forests and can exert cascading ecosystem effects, are sensitive indicators of ecological change, and are important culturally (Marcot and Johnson 2003, Whelan et al. 2008, McClure et al. 2018). Traits such as the regurgitation of undigested prey remains in pellets (Heisler et al. 2016) and the use of nest boxes by some species (Zárybnická et al. 2016) have facilitated studies of foraging habits and functional and numerical responses to changing prey populations (Korpimaki and Norrdahl 1991). Similarly, the relative ease of capturing and marking some species has facilitated extensive studies of habitat selection and demographics

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[1]*E-mail: cmw289@cornell.edu*
[2]*Contributed equally*

(Noon and Franklin 2002). Nevertheless, nocturnality generally precludes direct observations of owl behaviors such as hunting, mating, territory defense, and competitive interactions. This limitation has led to considerable uncertainties about owl behavioral ecology, factors regulating owl populations, and the magnitude of their ecosystem-level effects. Such knowledge gaps can have important consequences for conservation because, for example, foraging ecology can influence landscape-scale population dynamics (Hobart et al. 2019). Additionally, spatiotemporal variation in acoustic communication can affect prey populations (Eilam et al. 1999) and have implications for passive acoustic monitoring (PAM) programs designed to detect population changes (Wood et al. 2019*b*). Therefore, methods that can fill knowledge gaps would be valuable for research and conservation.

Recent advances in GPS technology and battery capacity and size provide new opportunities to study owl ecology because GPS tags can now provide minute-by-minute locational information with greater precision than previous generations of tags of comparable size (Marsh et al. 2014*a*, Blakey et al. 2019, San-Jose et al. 2019). The new generation of high temporal resolution (HTR) tags allow behaviors such as hunting and resting to be inferred by classifying locations based on the speed of movements, distance traveled, and turning angles (Marsh et al. 2014*a*, San-Jose et al. 2019), which was not practical with previous tags. However, inferring behavior from movement paths alone depends on the assumption that specific behaviors (e.g., hunting) are characterized by diagnostic flight speeds and directions. Alternatively, behaviors with similar movement paths can be aggregated into broad categories, but doing so requires grouping ecologically-distinct activities, for example, placing territorial vocalizations and resting into a single perching category (San-Jose et al. 2019). Thus, the full potential of new GPS-tag technologies may not be realized without applying complementary methods.

Here, we report how combining HTR GPS tags with other technologies can substantially improve our understanding of owl ecology. First, we demonstrate how arboreal video monitoring of the nests of HTR GPS-tagged owls enhances determination of the location of prey capture sites by identifying species brought to nests. Second, we show how the addition of on-board audio recorders to HTR GPS tags can be used to characterize the spatiotemporal vocalization patterns of individual owls, including the location where different calls are made. The methods we describe here have the potential to provide mechanistic explanations for critical aspects of owl ecology.

FORAGING ECOLOGY

Improving our understanding of owl foraging ecology is important because owls are apex avian predators that may exert wide-reaching ecological effects (Whelan et al. 2008), and because doing so can improve conservation outcomes (Hobart et al. 2019). High temporal resolution GPS tags used simultaneously with video surveillance of nest sites can allow researchers to identify with high precision both prey identity and locations of capture. Prey captures can be inferred from HTR GPS data when a tight cluster of sequential location points is followed by rapid but widely-spaced location points that lead directly to the nest, and can be confirmed as successful by video footage of a prey delivery to the nest site (Marsh et al. 2014*a*, San-Jose et al. 2019). To illustrate the feasibility of identifying prey and capture location in arboreally-nesting owls, we deployed HTR GPS tags (Alle-300, Ecotone Telemetry, Gdynia, Poland), programmed to record locations at two-minute intervals, for 4–12 days on five male California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada during May to June 2019. We captured owls by hand and with snare poles and we used tags weighing 11 g (~2% of the average body weight of a spotted owl), which we mounted on the two central retrices. Our settings yielded an effective battery life of 7–10 days. Birds were recaptured after 10–14 days and the tags removed so the data could be recovered. Birds jettison tail-mounted tags when they molt, ensuring that they are not subject to carrying the tag forever if they are not recaptured.

While the tags were deployed we monitored prey deliveries to females and dependent young at nests with infrared (IR) video cameras (Q1786-LE Network Camera, Axis Communications, Emdalavägen, Sweden) installed in adjacent trees. Male spotted owls regularly exhibited characteristic, straight-line flights from tight clusters of points, which we assumed to be indicative of foraging sites, back to nests where we recorded them delivering prey upon arrival (Fig. 1A). By using both HTR GPS data and nest video monitoring, we identified 54 locations associated with successful prey captures and identified prey in 36 cases (Fig. 1B). The number and species consumed included 21 woodrats (*Neotoma* spp.), 10 Humboldt's flying squirrels (*Glaucomys oregonensis*), 2 voles (*Microtus* spp.), 2 mice (*Peromyscus* spp.), and 1 pocket gopher (*Thomomys* spp.).

High temporal resolution GPS tags have been used in similar settings—notably in conjunction with in-nest video monitoring of burrowing owls (*Athene cunicularia*) (Marsh et al. 2014*a*, *b*) and nest-box video monitoring of barn owls (*Tyto alba*) (San-Jose et al. 2019). However, similar technology has not been used in conjunction with unobtrusive video monitoring of natural, arboreal nest sites typically selected by owls. We used the single-rope technique (SRT) (Perry and Williams 1981, Picart et al. 2014) to mount high-resolution IR video cameras 10–40 m above ground and 10–50 m from nest sites, thus mitigating observer effects induced by direct observation (e.g., in-nest cameras). The SRT method entails anchoring a static rope at the base of a tree and launching the line across a branch above the desired camera location and leaving one end of the rope hanging freely. We used an arborist harness, ascenders, a flip line (or some form of a backup system), and personal protective equipment (e.g., a helmet, gloves, and protective glasses) to reach the desired height. Once the camera was mounted, we used a belay device to lower the researcher

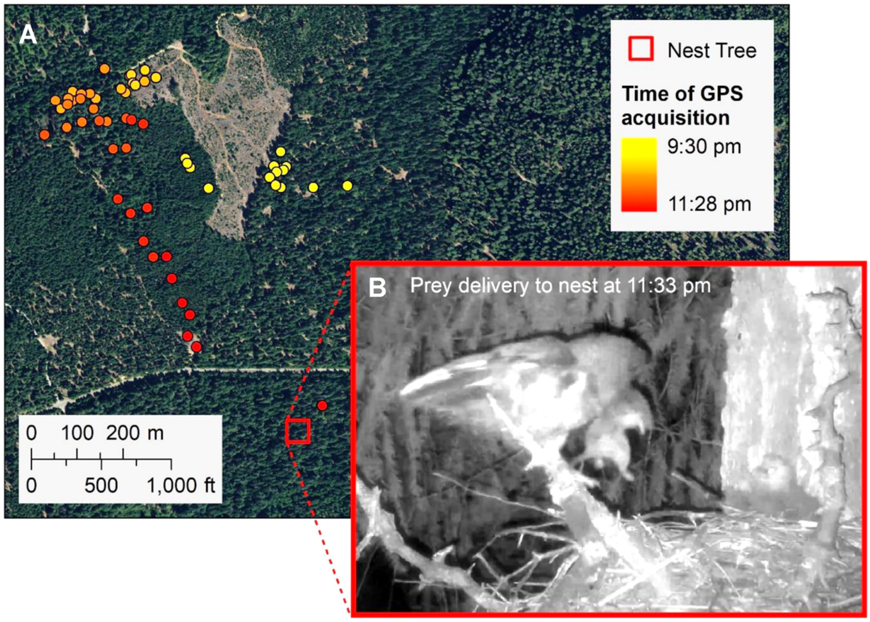

Figure 1. Map showing A) the sequence of owl HTR GPS locations for the two hours preceding a prey delivery, and B) an image of the subsequent prey delivery at the nest. The prey delivery image is a single frame from an infrared camera mounted 25 m above ground in a tree 40 m from the nest tree and shows the delivery of a woodrat to the nest and the waiting owlet in May 2019 in the central Sierra Nevada, USA. The approximate location of the capture could be inferred from the cluster of GPS locations before the owl's nearly direct flight back to the nest.

safely to the ground. The entire process took 4–5 hours depending on the height of camera placement, size of tree, and complexity of limb structure.

Deploying cameras in tall trees using the SRT method requires substantial training by a certified arborist. Nevertheless, using cameras has the potential to substantively improve our understanding of the foraging ecology of arboreally-nesting owls and of other large-bodied avian predators. The inferences drawn from resource selection functions (RSFs) without prey capture locations can differ substantially from those drawn from RSFs made with capture data yielded by HTR GPS tags and video cameras because prey-capture success may vary among habitat types in which owls forage (Marsh et al. 2014*a*). Because most studies do not consider known prey capture locations in RSFs, it raises the question of how well we actually understand owl foraging behavior. However, if enough prey deliveries are observed, researchers could develop individual RSFs for different species or categories of prey. Combining HTR GPS tags and video cameras to identify the habitat features that promote successful prey capture by owls and other raptors would provide opportunities to address many questions in ecology about how habitat influences predator-prey interactions.

Identifying patterns in prey capture locations may also contribute to improved raptor management by providing better estimates of microhabitat features that promote successful foraging. Foraging studies could be further enhanced by the incorporation of aerial LiDAR data, which can provide data at the resolution of individual trees and can characterize vegetation features at and below the canopy at the landscape scale. Thus, with HTR GPS tags capable of generating data with comparable spatial precision, we believe that the synergistic use of these two technologies could improve the conservation of owls.

ACOUSTIC ECOLOGY

Owls employ vocalizations for territorial defense, pair bonding, and other biological processes, and researchers commonly use such vocalizations to locate owls and monitor population status. Improving our understanding of the spatiotemporal patterns of vocal behavior can therefore benefit both basic and applied owl research. However, the use of conventional research methods such as VHF tags and handheld microphones cannot duplicate the spatial and temporal coverage, precision, and context of vocalizations that combining technologies enables (Finck 1990, Zuberogoitia et al. 2019). Consequently, we deployed novel HTR GPS tags equipped with onboard acoustic recording devices (Vesper 3.2, Alexander Schwartz Developments, Haifa, Israel) that were encapsulated in epoxy (Lotek Wireless, Wareham, UK) to collect locations at 1–2 minute intervals for 3–5 days on 8 spotted owls (4 males and 4 females) in the central Sierra Nevada. As before, owls were captured by hand and with snare poles and tags were mounted on the two central retrices. The tags weighed 11.6 g (~2% of the average body weight of a spotted owl) and our recording settings yielded an effective battery life of 3–4.5 days. Birds were recaptured after 7–8 days and the tags removed so the data could be recovered.

We then matched the recorded vocalizations to minute-by-minute GPS locations, allowing us to study owl vocal behavior at an unprecedented level of detail. We observed differences in the call rate, type, and timing, and in the location of calls based on sex and breeding status. Non-nesting owls, especially males, produced more territorial vocalizations ($\bar{x}_{\text{non-nesting male}} = 646$; $\bar{x}_{\text{nesting female}} = 3$) and were more likely to give calls throughout their range (Fig. 2A). In contrast, nesting spotted owls primarily produced nonterritorial calls indicative of communication between mates and between parents and offspring <300 m from their activity center; however, females provisioning fledglings were particularly vocal within that range ($\bar{x} = 801$ calls; Fig. 2B). Our findings suggest that further work has the potential to provide considerable insight to the sociobiological context of vocalizing spotted owls.

Deployment of HTR GPS tags with onboard audio recording capacity can create new opportunities to study acoustic communication in owls. For example, evidence suggests that owls face trade-offs when vocalizing during foraging. Spotted owls appear to reduce vocal activity in the preferred habitat of flying squirrels, a key prey species, possibly to mitigate prey vigilance (Wood et al. 2019*c*). In contrast, our data revealed that mated pairs of spotted owls employed and responded to vocal signals while foraging. Another trade-off with acoustic underpinnings is conducting territorial defense while avoiding conflict or predation. Spotted owls increase their territorial vocal activity (i.e., produce more four-note calls) in response to barred owls (*S. varia*), an invasive competitor, when barred owls are scarce (Wood et al. 2020). However, their vocal activity is reduced in response to barred owl calls when the latter species is common (Crozier et al. 2006). Thus, variation in time and space of territorial vocalizations may provide additional information about how species are affected by competition.

High temporal resolution GPS+audio tags allow estimation of the acoustic home range, or the area in which a species is vocally active (Fig. 2). Understanding spatiotemporal variation in the acoustic home range would be particularly valuable in the development of passive acoustic monitoring (PAM) programs, which typically use territorial vocalizations as indicators of site occupancy and can be implemented for multiple species simultaneously (Wood et al. 2019*a*, *b*). Therefore, HTR GPS tags also have the potential to provide a realistic estimate of an avian

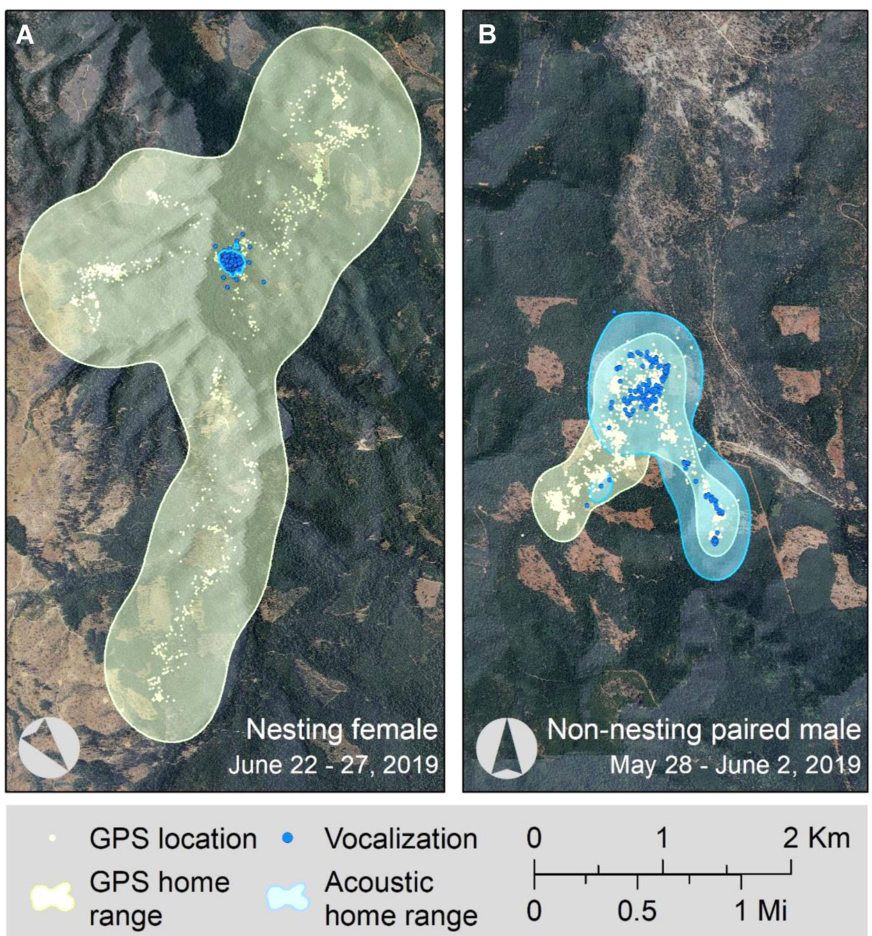

Figure 2. High temporal resolution GPS locations of spotted owls in the central Sierra Nevada, USA, and the locations of vocalizations, as well as traditional and acoustic home ranges, for A) a nesting female in late June, shortly after two young fledged, and B) a non-nesting male in late May. Differences in sex, nesting status, resource availability, and time of year of data collection all may have impacted the absolute and relative size and overlap of the acoustic and traditional home range. The home ranges were estimated using a 95% kernel density estimate of HTR GPS locations for physical location and location of vocalization.

predator's territory. Recent studies suggest that spotted owls regularly make forays into nearby, often unoccupied, territories (i.e., sites that had a history of occupation but were not occupied at the time of the forays) (Berigan et al. 2019, Blakey et al. 2019). However, if individuals are vocally active during extra-territorial movements, they could be recorded at multiple PAM survey sites that are assumed to be occupied by separate single or paired owls. Consequently, occupancy estimates would be biased high and important habitat associations could be obscured (Berigan et al. 2019). The spatiotemporal vocalization patterns revealed by estimating acoustic home ranges of relevant territorial vocalizations could inform the development of criteria to eliminate such false positive detections. Additionally, if vocalizations are found to be infrequent or spatially constrained in one or both sexes or during important reproductive stages, PAM could be ineffective if implemented at inappropriate scales, either because individuals simply would not be detected or because detection probabilities would be low and thus reduce statistical power to detect population change (Wood et al. 2019*b*). Therefore, HTR GPS+audio tag studies can be an important phase in the development of PAM programs for owls and other vocally active species.

CONCLUSIONS AND EMERGING FRONTIERS

We show that using HTR GPS tags in combination with other technologies has considerable potential to provide previously unattainable insights into the behavior of owls, as well as other raptors. Thus, many aspects of raptor ecology that have remained unstudied are now potentially open for scientific inquiry. Pairing HTR GPS tags with arboreally-mounted IR cameras can provide capture locations and identities of specific prey items of the many owl species that do not nest on the ground. High temporal resolution GPS tags with on-board audio recording devices can reveal variation in owl vocal behavior between sexes and breeding status, and across habitat and temporal gradients. This information could then be used to refine PAM projects designed to measure population change over time and in response to disturbance.

We encourage researchers to employ parallel methods that are less invasive and can be applied across broader areas. In this way, mechanistic understandings provided by tag data can be linked to broad-scale ecological patterns. For example, if spatial patterns in prey capture and delivery studies can be connected with stable isotope values, and if stable isotope analyses are conducted across a larger population, the results could be extended to entire landscapes (Hobart et al. 2019). Acoustic tag results could be used to inform studies that draw on landscape-scale passive acoustic survey data to study animal behavior (Wood et al. 2019*c*) and interspecific interactions (Wood et al. 2019*a*). The combinations of emerging technologies and methods that we have described here have the potential to resolve long-standing mysteries in owl ecology.

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