Non-visual camouflage predicts hunting success in a wild predator

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ABSTRACT

Predator-prey arms races have led to the evolution of remarkable disguise strategies. While the theoretical benefits of predator camouflage are well established, no study has yet been able to quantify its consequences for hunting success. High-resolution movement data therefore allowed us to study how barn owls (*Tyto alba*) conceal their approach when using a sit-and-wait strategy, as well as the power exerted during strikes. We hypothesized that hunting owls would reduce their landing force, and therefore noise, on perches located close to a hunting event. Analyzing 87,957 landings from 163 individuals equipped with GPS and accelerometer tags, we show that landing force predicts hunting success. Landing force also varied with the substrate, being lowest on man-made poles in field boundaries, most likely due to the opportunities for enhanced flight control in open landscapes. The physical environment therefore affects the capacity for sound camouflage, providing an unexpected link between predator-prey interactions and land-use. Finally, hunting strike forces were the highest recorded in any bird, relative to body mass, revealing the remarkable capacity of these predators to modulate their landing force and the range of selective pressures that act on landings. Overall, our results provide the first measurements of landing force in a wild setting revealing a new form of motion-induced sound camouflage, its link to hunting success and hence to fitness.

INTRODUCTION

Predation represents one of the strongest forms of selection in nature (1–6). As a result, animals have evolved sophisticated adaptations to modify the sensory information they emit (4,7–10) and alter their chances of capturing prey (11,12) or avoiding being caught (13–16). Camouflage has been widely studied as an anti-predator defense, with mechanisms including background matching, disruption, and self-shadow concealment facilitating predator avoidance (15). Predators also show adaptations to reduce detection by prey e.g. in their color, markings and/ or behavior (12,17). However, predator camouflage is far less understood due to the challenges of both simulating predation in controlled settings, and observing predation attempts in wild predators, which may also only alter their behavior in the final phase of a prey pursuit (18). This has hindered our understanding of the evolutionary forces driving predator camouflage and explains why predator cues have yet to be linked to prey capture success.

Predation typically requires movement of a predator towards its prey, either during a pursuit or the ambush that follows a period of sit-and-wait. However, motion makes individuals more conspicuous (5,19–21), rendering pursuit predators prone to detection. There is evidence that predators have evolved different camouflage strategies to reduce their chances of being spotted by their prey, although the direct link on hunting performance remains unclear (12,22). Many move slowly during the pursuit, which may provide camouflage, particularly when combined with background color matching (12,23,24). But motion also produces sound through the generation of vibrations and turbulences (25,26). Selection should therefore lead to sound minimization in quiet environments, explaining why many nocturnal species possess acute senses of hearing on which they rely to locate danger or prey (8,27,28).

The silent flight of owls is one of the most iconic examples of noise camouflage. Quiet flight is achieved through comb-like serrations on the leading edge of owls' wing feathers that break up the turbulent air and minimize associated sound production(29). While this might provide advantages when hunting on the wing, most owls also regularly hunt from a perch. This hunting technique involves the use of multiple perches to close in on prey and launch a final strike (30–32). In this rather dynamic sit-and-wait strategy, landing becomes a key element of the prey approach. But landing also produces vibrations and hence sound, with the intensity being proportional to the landing force (33). Using high-frequency GPS and accelerometer data from wild barn owls (*Tyto alba*), we quantify the landing dynamics of this sit-and-wait strategy to (i) examine how birds adjust their landing force with the behavioral and environmental context and (ii) test the extent to which the magnitude of the predator cue affects hunting success.

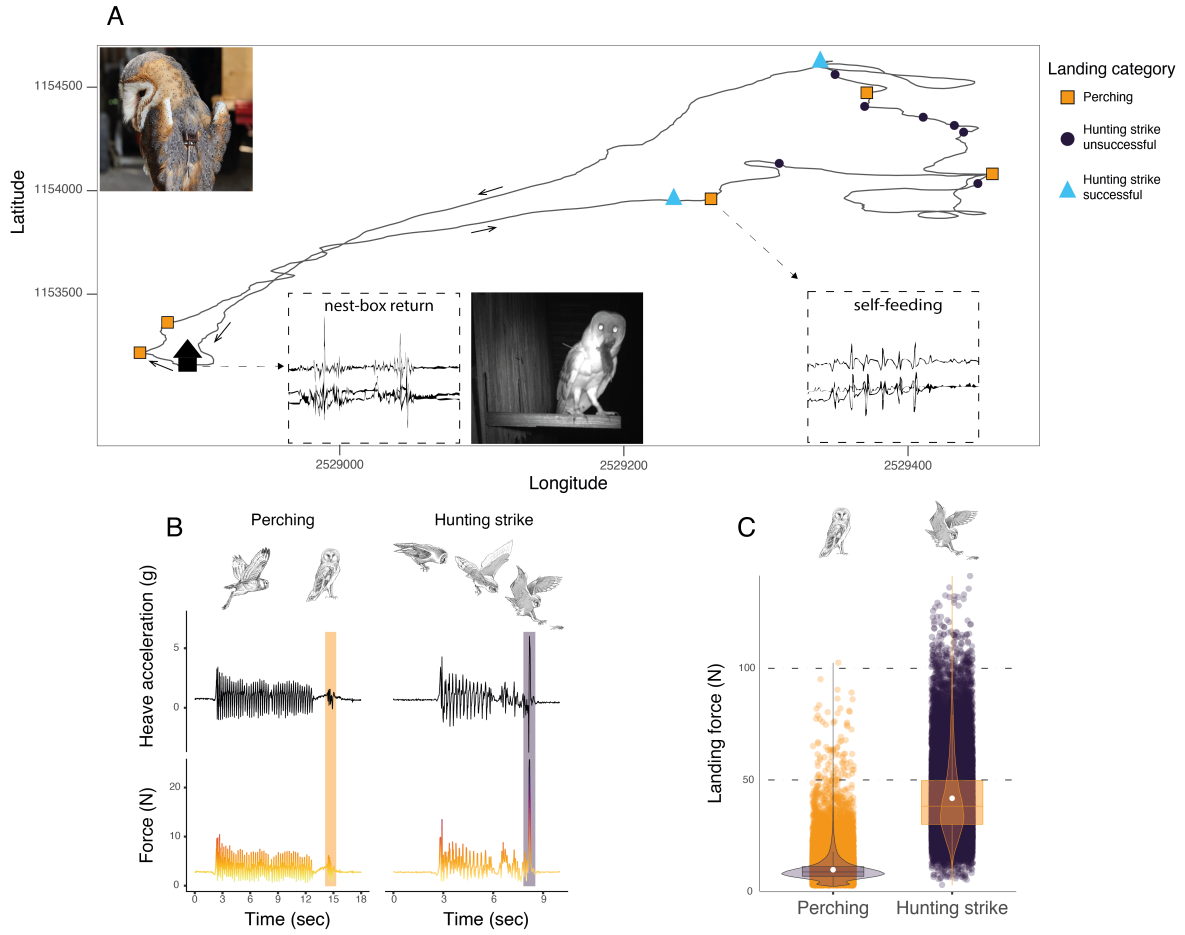

Figure 1. Sequence of perching and hunting strike events throughout a Barn owl foraging trip. A) GPS tracks during a typical barn owl foraging trip where perching events (squares) and both unsuccessful (circles) and successful (triangles) hunting strikes are shown. Black arrows indicate flight direction. Successful hunting strikes were identified by the presence of self-feeding events or by the direct return to the nest box (using the acceleration data, ground-truthed with the nest box camera footage). B) The heave acceleration and the estimated force during a perching event (highlighted in orange) and a hunting strike (highlighted in purple). C) Variation in peak landing force for perching events (orange dots, n = 56,874) and hunting strikes (dark dots, n = 27,981). White dots show the estimated mean, and data distribution is represented by both violin and box plots. Owl picture at the top left of Panel A is courtesy of J. Bierer, and owl drawings are courtesy of L. Willenegger, all used with permission.

RESULTS

Overall, we identified 84,855 landings (56,874 perching events and 27,981 hunting strikes) from 79 males (average body mass 281 g ± 16.5 SD) and 84 females (average body mass: 322 g ± 22.6 SD). The landing force varied significantly with the context, with hunting strikes having peak landing forces over four times higher than pre-hunt perching (Fig.1, Table S2; ratio: 4.5, z-ratio: 486.3, $p < 0.001$, with overall mean landing forces of 39.6 N, CI: 38.7 – 40.5 N, and 8.9 N, CI: 8.7 – 9.1 N, respectively). The peak forces in hunting strikes corresponded to c.a.13 times body weight, whereas pre-hunt landing forces were some three times body weight.

There was a significant interaction between sex and landing context, with female landing forces being 26% more than males during perching events (ratio F/M: 1.26, 95% CI: 1.2–1.31) but only 6% more during hunting strikes (ratio F/M: 1.06, 95% CI: 1.01–1.11, table S2). Our analysis of 27,981 hunting strikes showed that the strike force was greater for females than males (female 40.1 N, CI: 38.9 – 41.2 N; male 37.7 N, CI: 36.7 – 38.9 N). On average, males performed almost twice more hunting strikes per night than females (43.4 ± 13.5 SD vs. 23.7 ± 12.0 SD, respectively) but fewer perching events (65.7 ± 25.7 SD, and 71.7 ± 25.5 SD).

Landing force and hunting strategy predict hunting success

When hunting on the wing, successful strikes involved greater forces than unsuccessful strikes (n_{tot} = 24,464; successful strikes: 40.3 N, CI: 39.5 – 41.2 N, n = 5,830; unsuccessful strikes: 38.4 N, CI: 37.7 – 39.2 N, n = 18,634). This was not the case when barn owls hunted from a perch (n_{tot} = 3,517; successful strikes: 38.8 N, CI: 37.7 – 40.0 N, n = 1,042; unsuccessful strikes: 38.5 N, CI: 37.6 – 39.5 N, n = 2,475, Table S3).

Our model of hunting success, which included a subset of 3,040 hunting strikes from 151 individuals, showed that success varied with hunting strategy. When birds hunted from a post, hunting success was about 50% higher than when hunting on the wing (hunting success from a perch: 28.6%, CI: 25.7 - 31.7%; hunting success on the wing: 20.8 %, CI: 18.9 – 22.9 %). When hunting from the wing the force of the last landing had no effect on hunting success (odds ratio: 1.07, CI: 0.97 – 1.17, p = 0.19). In contrast, when owls launched an attack directly from a perch, a situation where the distance between the perch and the prey is rather short (median distance 6.5 m, Fig.S3), the pre-hunt landing force predicted hunting success (Fig.2, table S4), with the chances of success decreasing by 15% for every 1 N increase in landing force (odds ratio: 0. 85, CI: 0.79 – 0.99, p = 0.04). Perch type and wind speed were not significant predictors of success.

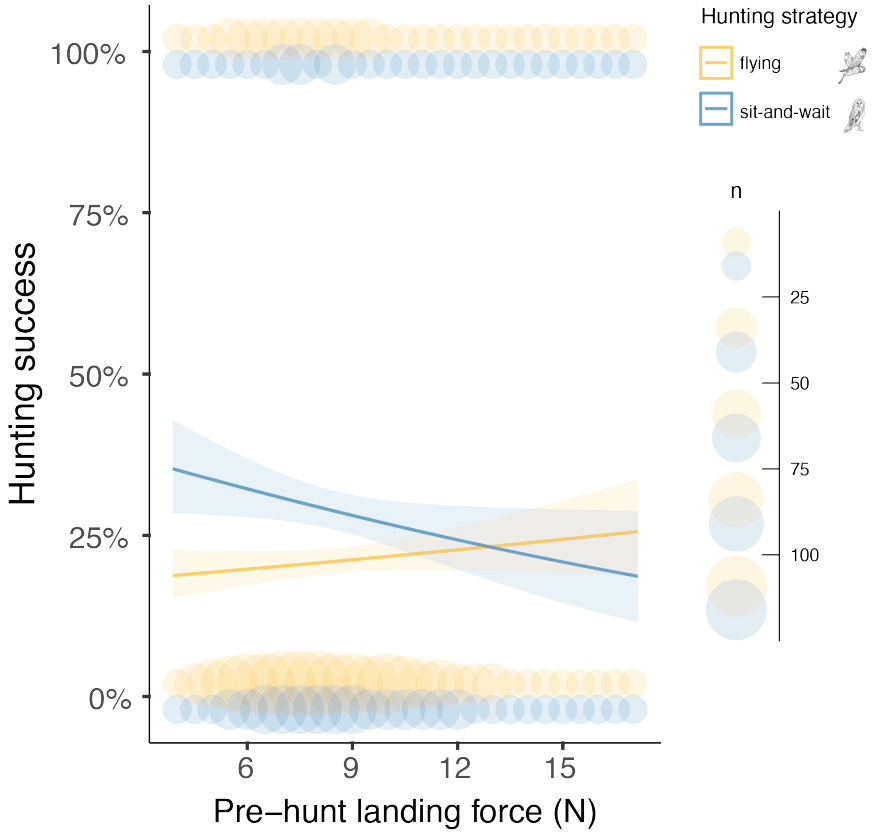

Figure 2. Pre-hunt landing force affects hunting success during sit-and-wait hunt. Variation in hunting success according to the pre-hunt landing force (N), depending on whether owls initiated strikes from the wing (yellow) or from a perch (blue). Solid lines show the estimated means (averaged over both sexes) and shades corresponds to the 95% confidence intervals around each mean. The owl illustrations at the top right are courtesy of L. Willenegger, used with permission.

Determinants of perching force

The landing force during perching was predicted by perch type, with landings on buildings having the highest forces (8.96 N, CI: 8.90 – 9.01 N), closely followed by landing on trees (8.86 N, CI: 8.81– 8.90 N; Table S5). Poles were associated with the lowest landing force (8.33 N, CI: 8.28 – 8.38 N). Within perch types, there was a reduction in landing force with time until the next hunting attempt, with the pattern differing with perch type (EDF_{poles} = 4.22, $p < 0.001$; $EDF_{buildings}$ = 1.00, $p < 0.001$; EDF_{trees} = 1.50, $p = 0.005$; Fig.3A, Table S4; n_{tot} = 40,306 perching events; see Fig.S4 for the full representation and derivatives plot): When barn owls landed on poles, the landing force showed a marked decrease in the last 30 minutes before hunting strike whereas force only showed a marginal linear reduction with time before strike for landings on buildings and did not show any significant reduction with time for landing on trees (Fig.3A, Fig.S4, Table S5). Furthermore, our analysis revealed a clear temporal pattern in the birds' use of perch types: the number of attacks launched from poles was greater than from trees, which was in turn greater than from buildings in the final moments before a strike (Fig.3B).

DISCUSSION

We used high resolution movement data to demonstrate that the magnitude of predator cues influences prey capture, with lower force, quieter landings (33), resulting in higher success for sit-and-wait hunts. Silent flight is thought to be critical for owls hunting on the wing. Sit-and-wait is also an important strategy, with owls in our study experiencing greater success when launching attacks from a perch (Fig.2, Table S4). Success is contingent on predators avoiding detection during both the approach and the landing, as the benefits of silent flight may be obviated if owls are detected at touchdown. While other predators, such as Orca (*Orcinus orca*), have been shown to reduce sound production during the final phase of a hunt (18), it has only been possible to infer the consequences for hunting success. We find that owls modulate their landing force in relation to their hunting behavior (Fig. 3A,3C) and show that this novel form of motion-induced sound camouflage has a direct link to fitness.

Landings are primarily governed by the need to maintain flight control and minimize the risk of injury (34–36). For instance, Harris' hawks (*Parabuteo unicinctus*) landing in controlled conditions postponed the stall until they were as close to the landing perch as possible (34). Such a strategy could serve two functions in sit-and-wait hunts by minimizing both the energy that is dissipated on impact and the associated sound production.

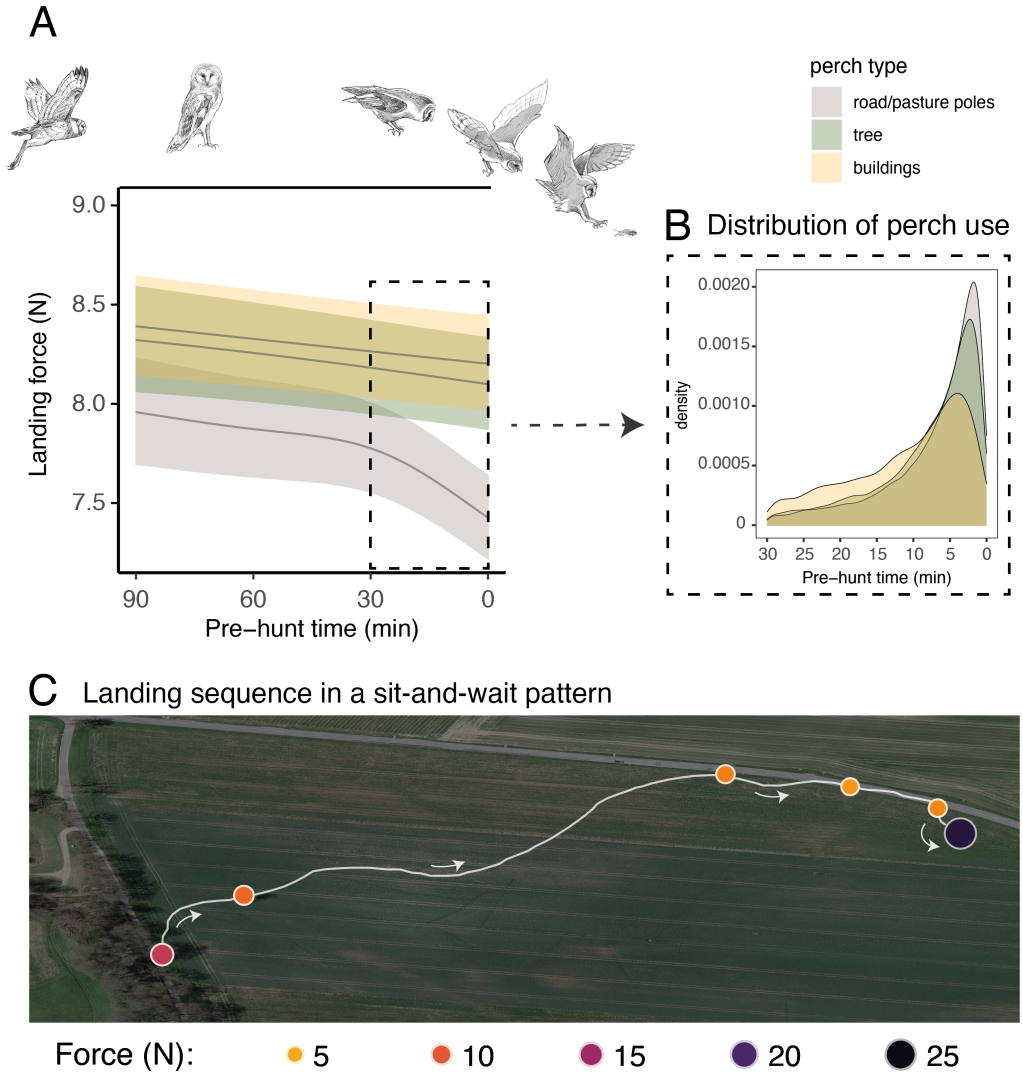

Figure 3. Sequential changes in perch type and reduction in landing force prior to hunting strikes during sit-and-wait hunt A) Landing force during perching events in relation to the time until the next hunting event and perch type. Each line represents the predicted mean for each perch type (here shown for males), with the 95% confidence intervals. B) The selection of perch type in relation to time until the next hunting strike, highlighting the change in perch type that occurs ~10 minutes prior to a strike. C) A sequence of perching events prior to a successful strike for a typical sit-and-wait hunt, showing the variation in peak landing force through time. White arrows indicate flight direction. The owl illustrations at the top of Panel A are courtesy of L. Willenegger, used with permission.

This raises the question of why owls would ever land with anything above the minimal force. To date, almost all studies have examined landings in controlled conditions (34,37), yet in the wild birds are faced with a range of perch types and landing conditions. Perch characteristics are likely to play a pivotal role, as forces tend to be absorbed to a greater degree by compliant substrates (38). In support of this, landings on buildings were associated with the highest mean forces, and higher forces than branches (Table S5), which will be more compliant, with the extent varying with e.g. the branch type and diameter. It was therefore notable that forces were lowest for landings on poles, which, like buildings, are rigid. Poles occur in open habitat, providing a predictable landing surface that can be approached from all directions, which facilitates control through optimal use of the wind vector. Landing force therefore appears to be influenced by the access options as well as the substrate type.

Owls also appeared to modulate their landings in relation to motivation and information on prey availability, as landing force decreased with the time before the next hunting attempt. Birds that landed on a perch a long time before a strike (30 – 90 minutes) may have done so without the immediate intention to hunt and hence have prioritized a different currency and/or perch type associated with greater landing force (Fig.3). The switch in predominant perch type from buildings to pasture poles that occurred 5-10 minutes prior to hunting strikes suggests this was a phase of active prey-searching. Yet, even here, we find a decrease in landing force as owls got closer to launching a strike. We propose this is an adaptive response to information on prey presence, with owls reducing their landing force as they moved ever closer to their prey suggesting that they are aware that a prey is around. Indeed, the perching phase itself may allow individuals to refine their estimates of prey location and gather additional information on prey type. This could explain the greater overall hunting success in attacks launched from a perch, compared to hunting on the wing. The fact that this final reduction in landing force was only achievable when owls landed on poles further highlights the importance of perch type and/or access. There may also be greater incentive to reduce landing force on poles, as sound attenuates with distance, and poles are close to the ground (29,39,40).

The biggest difference in landing force was seen between landing on perches and hunting strikes. Strike forces in our study are the highest recorded in any bird, relative to body mass, with maximal force reaching more than 34 times the bodyweight (100N). This exceeds those previously reported for captive barn owls (41), and the kicking strike of the secretary bird (*Sagittarius serpentarius*) that reached an average of 5.1 times body weight (42). Unlike secretary birds, whose kicking strength depends solely on the muscular power of their lower limbs, owls use the dynamics of their entire body in flight. While this minimizes the chances of prey escape, it is also associated with a potential risk of injury (34,43). Our results will be underestimates of the true peak forces, as acceleration was recorded at 50 Hz (data on force development in controlled car crashes are typically recorded at > 2 kHz). Nonetheless, our data can still provide new insight on the selective pressures that have influenced owl morphology. Indeed,

the lower limbs of owls allow for the dual function of absorbing shock during pre-hunting landings and generating extremely powerful hunting strikes.

In conclusion, the adaptive benefits of camouflage are well-established for prey. Here, we combine high resolution accelerometer with high resolution GPS data to gain insight into the selective pressures for predator camouflage. Specifically, we demonstrate that predator camouflage affects hunting success, with barn owls reducing their landing force to prevent detection by prey with an acute sense of hearing (27,28,44). Importantly, the ability to minimize landing force was modulated by the perch characteristics, providing a potential link between landing impact and habitat characteristics. Indeed, it suggests there could be spatial patterns in the effectiveness of acoustic camouflage and, ultimately, hunting success. The availability of different perch types could therefore be an additional, and previously unrecognized, aspect of habitat and territory quality, and, in this case, one that is strongly linked to land-use practices.

METHODS

Study area and tag deployment

Data were collected from wild barn owls breeding in nest boxes across the Western Swiss plateau, a region characterized by open and largely agricultural landscape (45). Over 380 nest boxes were checked for barn owl clutches between March and August in 2019 and 2020, following Frey and colleagues' protocol (46). During the two breeding seasons, 163 breeding barn owls (84 females and 79 males) were equipped with data-loggers (92 in 2019, 71 in 2020, Fig.S1). Adult owls were captured at their nest sites using automatic sliding traps approximatively 25 days after the first egg hatched. AXY-Trek loggers (Technosmart, Italy) were attached as backpacks (Fig.1A) using a Spectra ribbon harness (Bally Ribbon Mills, USA). These units include a GPS, set to record animal location at 1 Hz, 30 minutes before sunset until 30 minutes after sunrise, to get the full nightly activity period. The loggers also include a tri-axial accelerometer, which recorded acceleration continuously at 50 Hz (recording range ± 16g, 10-bit resolution). Each device weighed on average 12.3 g, representing less than 5% of bird body mass (47). Loggers were recovered after approximatively 15 days, with data recorded for 5 nights on average (± 1 night). Owls were weighed at both visits and the averaged body mass from the two measurements was used for later analysis.

In parallel to each logger deployment, motion sensitive camera traps (Reconyx HC500 hyperfire) were positioned at the entrance of all nest boxes to document when animals returned to the nest with prey (Fig.1A). Wind data were collected using portable weather stations (Vantage Vue, Davis Instruments corp.) mounted 2.0 m from the ground (standard anemometer measurement height) within 100 m of each nest. Wind speed and direction were recorded every 10 minutes.

Behavioral classification

We used Boolean-based algorithms (48) to classify flight, landing, hunting strikes, and self-feeding from the onboard acceleration and GPS data (see below). Behaviors were summarized in one-second intervals and linked to the closest GPS location in time. Flight, hunting, and self-feeding behaviors were ground-truthed using video footage of 2 captive barn owls equipped with the same data loggers. Further validations were undertaken for hunting behavior (detailed below).

Behavioral classifications used the raw acceleration data, the vectorial dynamic body acceleration (VeDBA) (a summary metric of body motion) and body pitch angle (Fig.S2, Table S1). VeDBA was derived by smoothing the raw acceleration data over 0.5 s (the period of two complete wingbeat cycles), to estimate the static/ gravitational component, subtracting this from the raw acceleration in each of the three acceleration channels (49), and calculating the vectorial sum from the resulting "dynamic" components. Pitch angle was derived using the arcsine of the static acceleration in the heave axis (50,51) and smoothed over 1 second.

Flights were identifiable from the acceleration data as periods of take-off, travelling and landing (Fig.S2A). Take-offs were characterized by a switch from a standing to a horizontal posture (Δ pitch angle > -10 °) and high-amplitude VeDBA (> 1 g) (41). Travelling flight was associated with smoothed VeDBA values > 0.1g, and body pitch values < 30 °. Finally, landings were identifiable as changes from low to high pitch angles (Δ pitch angle > 10 °) and a typical final spike in all three acceleration axes (VeDBA > 1 g). Periods that did not correspond to flight were categorized as stationary behavior.

Landings were further classified as either perching events, where owls landed on a perch prior to a hunting attempt or hunting strikes/prey capture attempts (Fig.1). Landing types were categorized using the rate of change in pitch angle (strikes: Δ pitch angle > 6 °) and the amplitude of the peak acceleration (strikes: Δ VeDBA > 1.3 g) generated by the impact with the prey/ground, which were both much greater for hunting strikes than perching events (Fig.S2B). Hunting strikes were classified using the Boolean-based classification algorithm (Table S1), whereas perching events were identified as the termination of flights that did not end with a hunting strike.

Owls hunt to provision themselves and their offspring. Self-feeding was evident from multiple and regular acceleration peaks in the surge and heave axes (resulting in peaks in VeDBA values > 0.2 g and < 0.9 g, Fig.S2D), with each peak corresponding to the movement of the head as the prey was swallowed whole. Prey provisioning were identified from variations in the sway, corresponding to the owl walking inside the nest box (Fig.S2C). Both start and end phases of the nest box visits were characterized by a rapid change in the pitch angle (enter: Δ pitch angle < -1.5 °; exit: < 0.5 °) along with an increase in the heave and VeDBA values (enter: Δ VeDBA > 0.5 g; exit: Δ VeDBA < -0.9), as owls leapt in/out of the nest box. Successful provisioning hunts were further confirmed using nest box camera data when available and, in all cases, by manually

checking that the GPS data matched the nest site to identify cases where the owls returned with a single prey for their offspring. Unsuccessful strikes were therefore inferred from identified hunting strikes that were not followed by a provisioning to the nest and/or self-feeding event (Fig.1A).

Data processing

Data from the onboard accelerometers can be used to estimate landing force during perching and hunting strikes (Fig.1B), as force is equal to the product of mass and acceleration. To estimate landing force, we extracted the peak vertical component of the ground reaction force in Newtons (N) for every landing event, taking the maximum value of the vectorial sum of the raw acceleration (in units of gravitational acceleration, *g*), multiplying this by the body mass of the bird (in kg) (52,53).

Hunting strikes were categorized according to whether owls hunted on the wing or from a perch to assess factors affecting the landing force of perching events involved in the sit-and-wait strategy. We therefore considered that owls were using the sit-and-wait strategy if they flew for a maximum of 1 second before the strike (corresponding to c.a. 6.5 m from the last perch). Hunting on the wing was defined as cases when birds flew for at least 5 seconds prior to the strike (c.a. 81.7 m from the last perch). Hunting strikes that did not fit into either category (8% of all hunting strikes) were excluded from the dataset.

Finally, perch type was estimated by extracting the median location of each perching event. The habitat within 2 m was then classified according to the main perch type available: trees, roadsides and pasture poles (hereafter referenced as “poles”), and buildings, and assigned as the perch type for each perching event. Habitat categories (roads, settlements, single trees, forest) were provided by the Swiss TLM3d catalogue (Swiss Topographic Landscape Model, resolution 1-3 m depending on the habitat feature) and land use data were provided by the “Direction générale de l'agriculture, de la viticulture et des affaires vétérinaires (DGAV)” and the “Direction des institutions, de l’agriculture et des forêts (DIAF)”, for states of Vaud and Fribourg respectively.

Statistical analyses

We first assessed how landing force varied between hunting strikes and perching events, before evaluating the factors that explained variation within each category. This excluded perching events made when owls were loaded with prey, where the landing force will likely be influenced by the extra mass carried.

We fitted a linear mixed model (LMM) of the landing force (log-transformed) where fixed factors included the landing context (a two-level factor: hunting strike or perching event), the sex of the individual (a two-level factor: Female and Male) and their interaction. Sex was included in the model to account for sexual differences in foraging strategy as well as a sexual dimorphism in body mass (31). Wind speed was

also included as fixed factor in the model, along with its interaction with landing context, as wind speed has been shown to affect landing success in birds (54) . The model included bird ID as a random intercept to account for repeated measurements of the same individual over multiple nights, and night ID (nested in bird ID) to account for repeated measurement of the same individual within the same night. The same random effect structure was applied to all the following LMs and GLMs as they were fitted to dataset of similar grouping structure. We next fitted a LMM of the landing force during hunting strikes (log-transformed). Fixed factors in the model included hunting success (a two-level factor: successful and unsuccessful), the hunting strategy (a two-level factor: perching and flying) and their interaction. Sex was also included as a fixed factor.

To test whether landing force during perching influenced the success of the next hunting strike, we performed a generalized linear mixed-effect model (GLMM) with hunting success as a binary response variable. The fixed effects included landing force, hunting strategy and their interaction, individual sex and windspeed. Hypothesizing that landing force affects barn owl detectability, we only selected hunting strikes that were immediately preceded by a perching event (hereafter pre-hunt perching). We also selected hunting strikes that occurred < 1.5 minutes after the last perching event to maximize the probability of capturing a response to the pre-hunt landing force. The threshold of 1.5 minutes corresponded to the lower tercile of the distribution of time differences between perching and hunting strikes.

Finally, we fitted a generalized additive mixed-effects model (GAMM) to assess how the landing force (log-transformed) varied between perching events. Specifically, we examined whether this was affected by the physical environment (perch type, wind), or motivation (owls can perch for long periods between hunts, and the most pertinent currency determining landing force may therefore vary between periods of resting and active searching). Time until the next hunting strike was extracted for every perching event and included as a continuous fixed covariable in the model. An interaction between a smoothed function of the time until the next hunting strike and perch type was also included, using a thin plate regression spline and the “by” condition, with the number of bases per smooth term (k) set at a conservative value of 9. The sex of the individual, windspeed and perch type (a three-level factor: pole, tree, building) were included as linear predictors in the model. The model included the random intercept effect of bird ID (included with bs=”re” in a smooth function).

Our GAMM of landing force showed that owls perched more softly the closer they came to the next hunting strike. To identify periods when there was a significant change in landing force, we calculated the first derivative $f`(x)$ of the estimated smoothed relationship between the time to the next strike and the peak landing force, according to each perch type, to highlight significant periods of positive or negative relationships (55,56). Periods of significant change were identified as those time points where the simultaneous confidence interval on the first derivative does not include zero.

All statistical analyses were conducted with R 4.0.5 (R Core Team, Vienna, Austria), with RStudio (RStudio Team, 2020) as graphic user interface. LMMs and GLMMs were fitted with the functions *lmer* and *glmer*, respectively, implemented in the package 'lme4' (R package v1.1-27.1) (57) and we used the package 'lmerTest' (R package v3.1-3) (58) to estimate p-values. GAMM model was fit using the *gam* function from the package 'mgvc' (R package v1.8-34) (59–61). For all models, linear predictors were centered and scaled to mean zero and units of standard deviation (i.e., z-scores) to ensure comparability among variables. We performed pairwise comparisons using the *emmeans* function from the package 'emmeans' (R package v1.6.0) (62) to further assess differences between predictors level. Models were fitted, checked for collinearity between predictors and assumptions were verified by visually inspecting residual diagnostic plots. Non-significant terms were dropped via model simplification by comparing model AIC with and without terms. Descriptive statistics are reported as Mean ± SD, unless specified otherwise.

Ethical statements

This study meets the legal requirements of capturing, handling, and attaching GPS devices to barn owls in Switzerland from the Department of the consumer and veterinary affairs (legal authorizations: VD, FR and BE 3213 and 3571; capture and ringing permissions from the Federal Office for the Environment).

Data availability

The datasets and codes generated and/or analyzed during the current study will be available from the date of publication without restrictions.

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Competing interests

The authors declare no competing interests.