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Differential fitness effects of moonlight on plumage colour morphs in barn owls

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The Moon cycle exposes nocturnal life to variation in environmental light. However, whether moonlight shapes the fitness of nocturnal species with distinct colour variants remains unknown. Combining data from long-term monitoring, high-resolution global positioning system tracking and experiments using prey, we show that barn owls (*Tyto alba*) with distinct plumage colourations are differently affected by moonlight. The reddest owls are less successful at hunting and providing food to their offspring during moonlit nights, which associates with lower body mass and lower survival of the youngest nestlings and with female mates starting to lay eggs at low moonlight levels. Although moonlight should make white owls more conspicuous to prey, it either positively affects or does not affect the hunting and fitness of the whitest owls. We experimentally show that, under full-moon conditions, white plumage triggers longer freezing times in prey, which should facilitate prey catchability. We propose that the barn owl's white plumage, a rare trait among nocturnal predators, exploits the known aversion of rodents to bright light, explaining why, counterintuitively, moonlight has a lesser impact on the whitest owls. Our study provides evidence for the long-suspected influence of the Moon on the evolution of colouration in nocturnal species, highlighting the importance of colour in nocturnal ecosystems.

Colouration largely determines how animals interact with their biotic and abiotic environments[1]. Perception of an individual's colouration by conspecifics, predators and prey depends on the reflective properties of an individual's colour, its environmental background, the viewer's visual system and the environmental light[2,3]. The latter component might shape the evolution of colouration, with heterogeneous light conditions favouring distinct colourations, as shown, for instance, in African cichlid fish living at different depths[4,5] and in birds exploiting the canopy or the understory of tropical forests, inhabiting less or more cloudy environments, or nesting in the open or in dark tree cavities[6–8]. However, most of the studies linking variation in environmental light and organismal colouration come from diurnal species, and the consequences of variation in nocturnal light on the evolution of animal colouration are barely known[9].

The Moon has shadowed the evolution of life, which adapts its endogenous rhythms to the lunar cycle[10–14]. Moonlight alters the activity patterns of animals[15–18] because it alters an individual's capacity to visually detect food or to remain concealed[19–22]. By producing contrasting changes in light conditions[23], the Moon might also drive the evolution of colouration in nocturnal animals, but this hypothesis has received little attention despite being proposed more than one hundred years ago[24]. It is difficult to observe behaviour in nocturnal species[25], and in addition, some authors have suggested that our limited night vision has 'clouded' our expectations of the importance of colour and light variation for nocturnal species[26]. This could explain why the colouration of nocturnal species has often been considered to be an adaptation for diurnal camouflage rather than for a nocturnal life[27].

In line with the accumulation of studies highlighting the importance of colour vision in nocturnal species[23,28,29], a few recent studies have indirectly addressed how nocturnal light variation relates to animal colouration. Cuttlefish, *Sepia apama*, actively adapt their colour patterns to their background not only during the day, but also during the night[25,30]. Eagle owls, *Bubo bubo*, call more often during full-moon nights when their white throat patches, a potential visual signal[31], seem to be more consipicuous[32]. Colour polymorphism is more common in owls living in light-heterogeneous habitats formed by both forested and open landscapes[33]. Variation in nocturnal light levels might thus act as a selective agent on animal colouration. However, evidence supporting the notion that moonlight variation affects the fitness of individuals with respect to their colouration is still lacking.

By combining data from a breeding population monitored over the last 20 years with high-resolution global positioning system (GPS) tracking, we investigated how moonlight affects foraging, as well as the success and timing of breeding, in barn owls, in which genetic variation produces ventral plumage ranging from white to dark red[34,35] (Fig. 1). To identify the mechanism behind colour-specific performance in barn owls, we experimentally investigated the antipredator response of the barn owls' main prey, the common vole (*Microtus arvalis*), when exposed to white and red owls under different moonlight conditions. The adaptive role of the red and white plumage of barn owls remains unknown. Some previous studies have used genetic models to discard that colour variation in this species follows the expectation of a neutral trait[36,37], while other studies have suggested that colour variation may have a role in predator–prey dynamics[38,39]. Because light variation might affect the ability of prey to visually detect predators[10], we predict that moonlight influences owl hunting efficiency and, thereby, breeding success and timing. Rodent prey are likely to perceive different

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Fig. 1 | Colour variation in barn owls. Barn owls exhibit continuous variation in plumage colouration, from white to dark reddish. Credit: Isabelle Henry

owl plumages as different shades of grey (that is, as differences in luminance), with the less-reflective plumage of red owls appearing darker than white plumage[40,41]. Similar to other vertebrates with duplex retinae, rodent prey probably rely on sensitive but colourless rod vision[28]. Even if some rodent species have up to two cone types[42] and might see colours, the rodents' chromatic vision, in addition to luminance, should make red owls appear less conspicuous than white owls. Thus, we expect that barn owls should be more conspicuous during full-moon nights and exhibit a lower foraging success. This negative effect of moonlight should be stronger in white than in red owls because white plumage is expected to reflect light more efficiently. We expect smaller differences during new-moon nights because limitation of dark noise in dim light is likely to result in less contrasted differences between red and white owls[28].

Results

Effect of plumage colouration and moonlight on food provisioning and hunting success. Using infrared cameras, we first investigated whether parental colour and moonlight (measured as the visible percentage of the Moon; see Methods and Supplementary Fig. 1) affect food provisioning (the total number of prey that adults brought to their offspring each night). On average, food provisioning was 4.78 prey per night ± 1.22 (standard error, s.e.) and was significantly associated with moonlight in interaction with parental colour (Poisson generalized linear mixed model (GLMM): $z = -2.33$, $P = 0.02$; Supplementary Table 1 and Fig. 2a). The food provisioning of the reddest parents decreased from new-moon (5.67 prey ± 1.21) to full-moon (3.27 prey ± 1.25; $z = -3.72$, $P < 0.001$) nights. There was no significant relationship between food provisioning and moonlight in the whitest parents ($z = -0.81$, $P = 0.42$), who brought 4.94 ± 1.21 and 4.61 ± 1.22 prey during new- and full-moon nights, respectively.

Hunting success, as measured in males equipped with GPS trackers, significantly depended on the interaction between plumage colouration, moonlight and hunting effort (Supplementary Table 2). We observed no effect of moonlight and plumage colouration on hunting success when owls performed a below-the-mean hunting effort (<26 hunting events per night, binomial GLMM: $z = 0.54$, $P = 0.588$). When the owls' effort was above the mean, hunting success in the reddest owls decreased from 0.48 ± 0.3 (s.e.) at new-moon nights to 0.42 ± 0.2 at full-moon nights (plumage colouration × moonlight: $z = -2.28$, $P = 0.023$, contrast within the reddest owls: $z = -2.34$, $P = 0.019$, Fig. 2b). No significant effect of moonlight was detected within the whitest owls ($z = 1.45$, $P = 0.147$, Fig. 2c). Owls do not adjust their hunting effort to moonlight or plumage colouration, but moonlight affected at which time of the night the owls hunted (Supplementary Table 3 and Supplementary Fig. 2).

Effect of plumage colouration and moonlight on prey anti-predator behaviour. To investigate why full- and new-moon light conditions have different effects on the parental food provisioning and hunting success of white and red owls, we experimentally investigated how common voles (the staple prey in our owl population[38]) detect and react (by either freezing or fleeing[43,44]) to red and white taxidermized barn owls under light conditions mimicking full- and new-moon nights (see Methods). Regardless of owl colouration, the probability of vole response to the owls was 0.49 ± 0.07 (s.e.) under the full-moon conditions and was significantly smaller at 0.20 ± 0.05 under the new-moon conditions (binomial GLMM: moonlight: $\chi^2 = 31.36$, degrees of freedom (d.f.) = 1, $P < 0.0001$, owl morph: $\chi^2 = 0.03$, d.f. = 1, $P = 0.862$, interaction: $\chi^2 = 0.58$, d.f. = 1, $P = 0.447$; Supplementary Table 4 and Fig. 3a).

Voles responded to the owls mainly by freezing (83% of the trials). The time they spent frozen was on average 9.5 sec ± 1.3 (s.e.), and the amount of time significantly depended on the interaction between owl colouration and moonlight (LMM: $t_{41.78} = 2.02$, $P = 0.049$, Supplementary Table 4). Under full-moon conditions, voles froze for 5.15 sec ± 1.6 longer when facing a white owl rather than a red owl ($t_{47.46} = 2.42$, $P = 0.039$), and voles froze for 9.6 sec ± 2.0 longer when facing a white owl under full-moon compared to new-moon conditions ($t_{47.41} = 3.59$, $P = 0.003$, Fig. 3b). No significant differences were found between white and red owls under new-moon conditions ($t_{39.50} = -1.10$, $P = 0.368$) or in response to red owls under full- and new-moon conditions ($t_{56.26} = 0.85$, $P = 0.424$).

To confirm that the increased freezing times observed were caused by the amount of light reflected from white plumage during full-moon conditions, we experimentally tested the prediction that voles should spend less time frozen after facing a white owl of reduced plumage reflectance. To test this, we masked the plumage reflectance of one mounted white owl by applying duck preen wax (CDC) to its feathers (see Methods, Fig. 3c). Under full-moon conditions, decreased plumage reflectance resulted in significantly shorter freezing times in voles (13.6 sec ± 1.2 (s.e.)) than those produced by white plumage without CDC (26.4 sec ± 1.2, LMM, moonlight $\chi^2_1 = 5.56$, $P = 0.018$, CDC treatment: $\chi^2_2 = 21.69$, $P < 0.001$, interaction: $\chi^2_2 = 21.24$, $P < 0.001$, contrast under full-moon conditions: $t_{24.05} = 4.66$, $P < 0.001$; Fig. 3d). No differences were found under new-moon conditions ($t_{6.21} = 1.35$, $P = 0.223$).

Effect of moonlight and parental colouration on nestling mass and survival. We investigated the potential fitness consequences of the effect of moonlight and plumage colouration by testing whether offspring body mass and fledging success reflect the effects observed in food provisioning. The offspring body mass depended on the moonlight in interaction with the father's colour (LMM: $\chi^2_1 = 4.49$, $P = 0.034$; Supplementary Table 5). Consistent with the patterns of food provisioning, the offspring mass decreased from new-moon (224.1 g ± 2.2 (s.e.), estimated at the mean nestling age (30 d)) to full-moon nights (220.7 g ± 2.3) in nests raised by the reddest fathers ($\chi^2_1 = 4.49$, $P = 0.04$, Fig. 4a,b). The body mass of owlets raised by the whitest males was not significantly different from new- to full-moon nights (228.0 g ± 1.5 and 228.8 g ± 1.5, respectively, $\chi^2_1 = 2.23$, $P = 0.13$). Thus, the major differences between colour morphs occurred during full-moon nights (6.6 g ± 1.0, $\chi^2_1 = 5.37$, $P = 0.021$) but not during new-moon nights (2.3 g ± 1.0, $\chi^2_1 = 0.36$, $P = 0.55$).

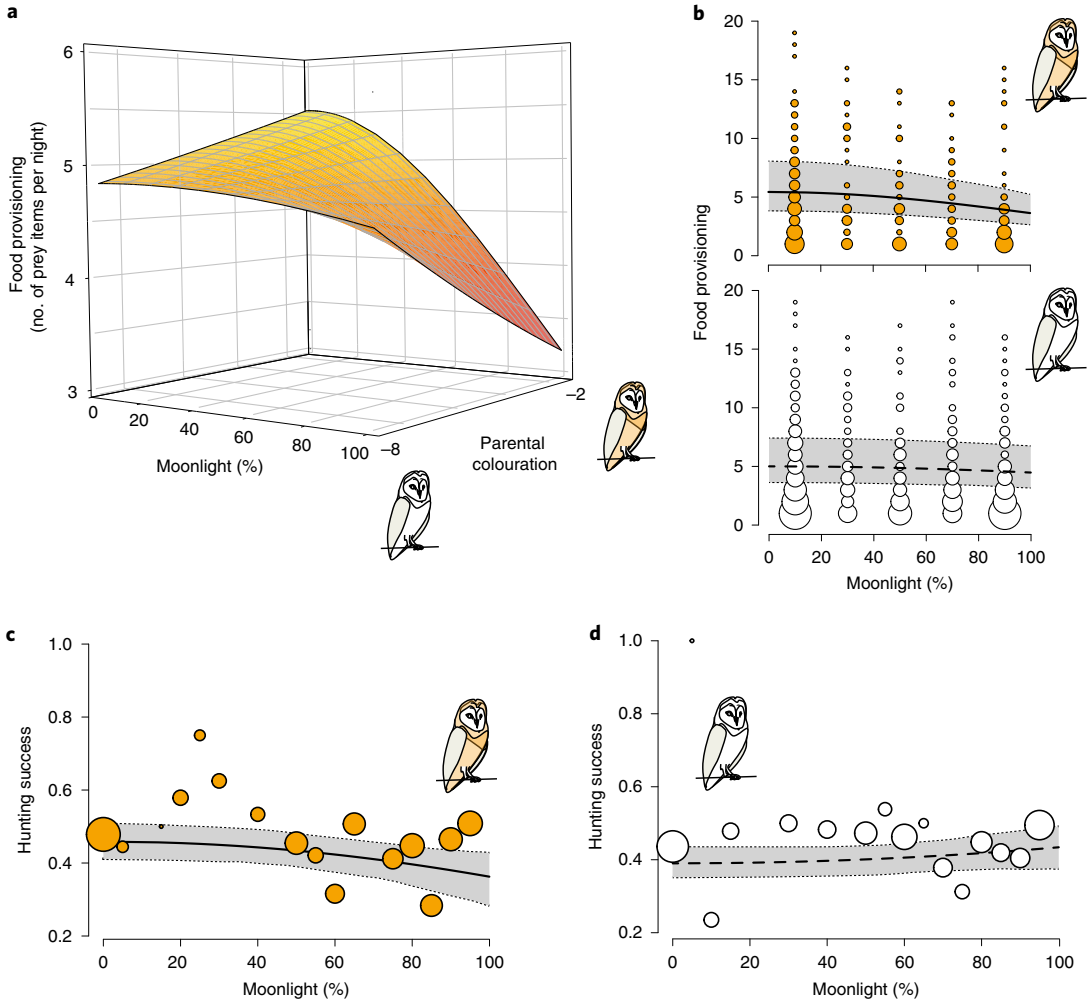

Fig. 2 | Parental food provisioning depends on moonlight and parental plumage colouration in the barn owl. a, Relationship between the total number of prey items brought by male and female parents and plumage colouration in interaction with moonlight. The predicted surface from a Poisson GLMM is presented. **b**, Detailed effects of moonlight on food provisioning. Shown are the observed values of food provisioning (pooled every 20 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 77 observations), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval (grey shaded area) for barn owls above the third quantile (reddest owls) and first quantile (whitest owls) of colour variation. **c**,**d**, Hunting success within the reddest (**c**) and whitest owls (**d**). Shown are the observed values of hunting success (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 694), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval for barn owls above the third quantile (reddest owls) and first quantile (whitest owls) of colour variation.

We observed no effect of the moonlight and father plumage colour on fledging success (binomial GLMM: $\chi^2_1 = 0.04$, $P = 0.52$, Supplementary Table 6). However, due to a marked age hierarchy (rank) among barn-owl siblings, with first-born (high-rank) nestlings exhibiting highest survival probability (above 75%; Supplementary Fig. 3a), we expect the youngest nestlings to be more affected by reduced food provisioning. When only low-ranking offspring (rank ≥ 7) were considered, fledging success depended on the moonlight in interaction with father colouration (quasibinomial GLMM: $t_{62} = -2.58$, $P = 0.012$, Supplementary Table 7). From new- to full-moon nights, fledging success increased in nestlings raised by the whitest parents (from 0.35 ± 0.2 (s.e.) to 0.95 ± 0.1, $t_{62} = 3.03$, $P = 0.008$), while it tended to decrease in nestlings raised by the reddest parents (from 0.61 ± 0.3 to 0.14 ± 0.1, $t_{62} = -1.97$, $P = 0.071$; Fig. 4c,d). When accounting for cloud cover, which can mask moonlight effects (see Methods), the contrast remained significant for the whitest parents ($t_{61} = 3.65$, $P = 0.001$) and became significant for the reddest parents ($t_{55} = -2.09$, $P = 0.040$) (Supplementary Table 8).

Association between plumage colouration and moonlight and breeding. We observed a significant negative association between male colouration and the moonlight levels on the night a male's mate laid the first egg ($z = -2.87$, $P = 0.004$, Supplementary Table 9a). Females that mated with the whitest males had a higher probability of laying the first egg of their clutch (0.58 ± 0.02 (s.e.)) during nights with at least 50% of the Moon's surface illuminated, whereas females who mated with the reddest males had a higher probability of laying the first egg (0.62 ± 0.06) when less than 50% of the Moon's surface was illuminated (Fig. 5). Given the Moon cycle of roughly 29 d, we can expect similar negative associations between moonlight and plumage colouration at other moments of the barn owl's breeding cycle; more relevantly, when the first in-nest copulations are expected to occur (~27 d before laying the first egg[45], $z = -2.27$, $P = 0.023$), and when nestlings of rank 6–8 are expected to reach an age of 15 d old (between 59 and 63 d; roughly 2 moon cycles after a female laid the first egg: $z = -2.61$, $P = 0.009$, Supplementary Table 9b, c).

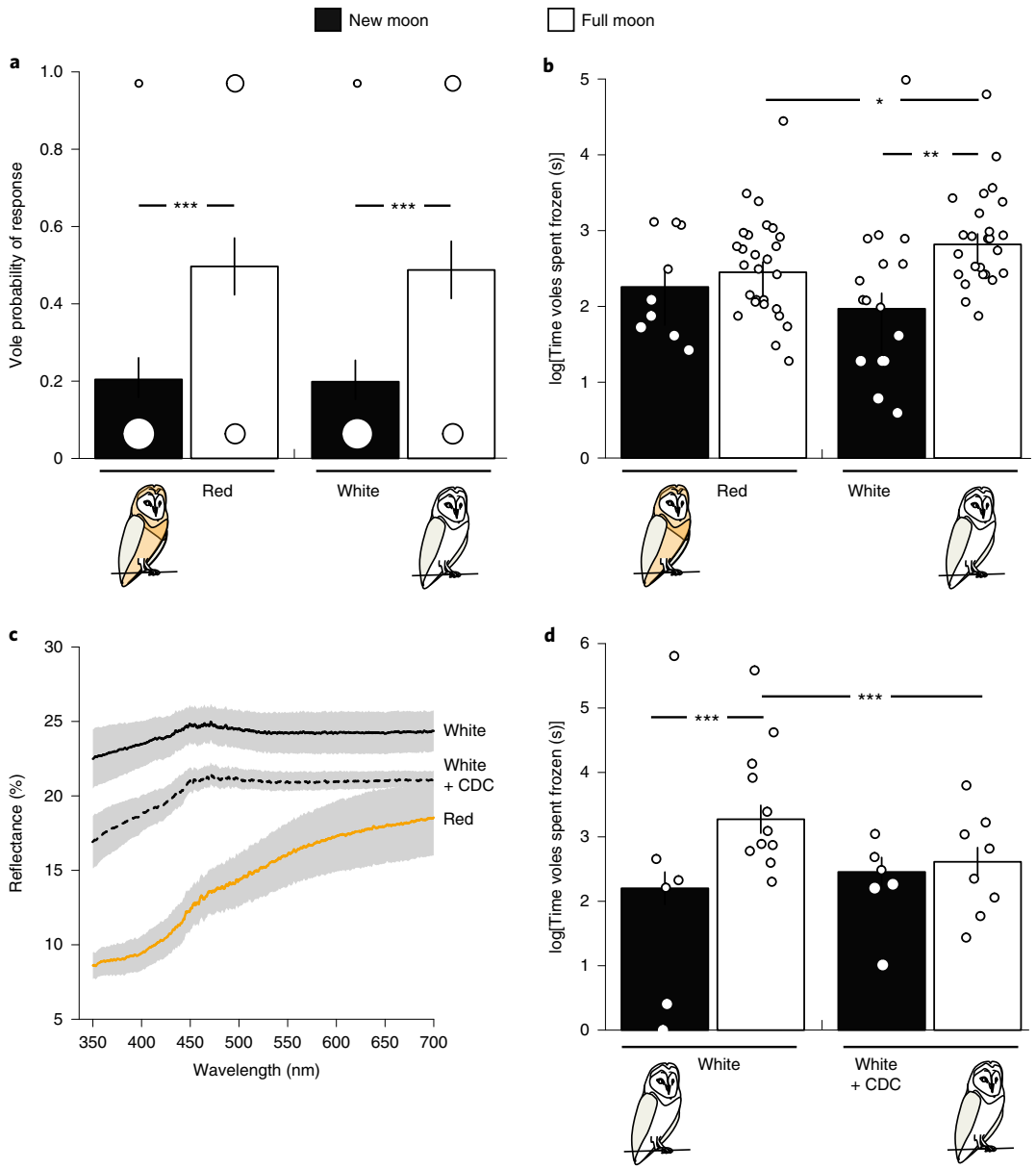

Fig. 3 | Probability of response and time spent frozen of common voles as a function of barn-owl plumage colouration and moonlight conditions. **a**, Probability (± s.e.m.) that common voles detected (and exhibited either freeze or flee behaviour) stuffed owls of white and red colour under light conditions mimicking full- and new-moon nights. The size of the white dots represents the number of observed responses of the voles (smallest dots = 21 observations, largest dots = 85 observations). **b**, Time (± s.e.m.) voles spent frozen (immobile) after observing white and red owls under light conditions mimicking full- and new-moon nights. **c**, Mean reflectance spectra (± s.e.m.) of the plumage of a white owl, a white owl treated with CDC wax and a red owl. **d**, Time (± s.e.m.) voles spent frozen (immobile) after observing a normally coloured white or a white owl treated with CDC under light conditions mimicking full- and new-moon nights. $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$.

Discussion

Our study shows that the Moon differently affects the hunting performance and the reproductive success and timing of barn owls with contrasting plumage colourations. This supports the long-standing, untested hypothesis that moonlight influences colouration of nocturnal animals[9,24,30], particularly by uncovering a link between fitness proxies, moonlight and colouration that was missing in previous studies[25,32]. Moreover, our study raises the possibility that the unique white colouration of barn owls might be favoured by moonlight owing to the effect that the light being reflected from white plumage has on the prey's behaviour.

The reddest owls show diminished food provisioning and hunting success on full-moon nights (Fig. 2a,c). Lower hunting success and food provisioning of the reddest owls during full-moon nights can be explained by the higher probability of voles detecting owls under full-moon conditions (Fig. 3a). The effect of the moonlight on hunting performance has a mirroring effect on reproductive success. In owlets raised by the reddest owls, body mass decreases from new- to full-moon nights, in line with the reddest parents bringing more prey during new-moon nights than during full-moon nights. Consequently, the survival prospects of nestlings raised by the reddest parents were lower when maximal nestling growth occurred during full-moon nights (when owlets received less food and weighed less). Survival impairment was only evident in the youngest chicks (age rank ≥ 7), probably because their smaller size made them more vulnerable than their older siblings[46].

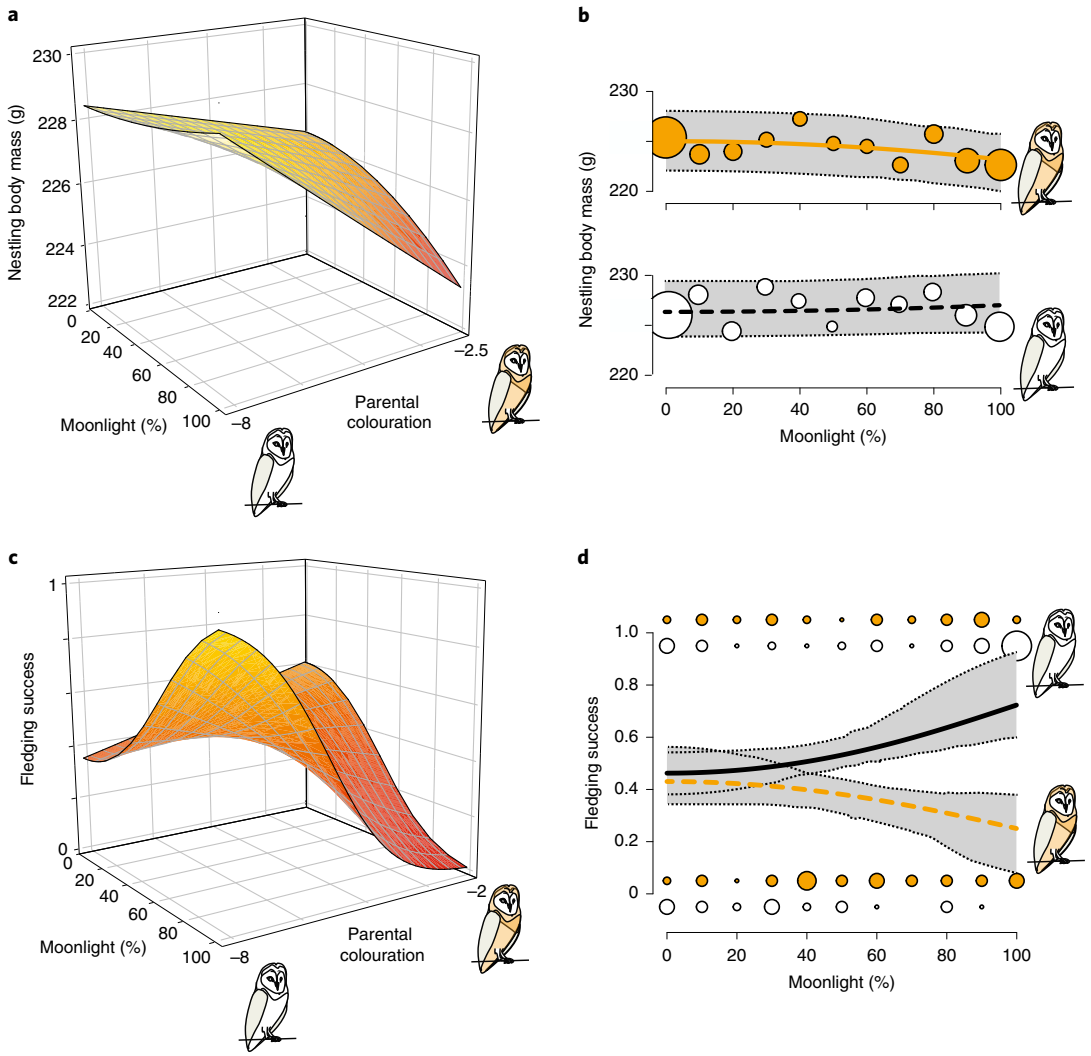

Fig. 4 | Offspring body mass and survival depend on moonlight and parental plumage colouration in the barn owl. a, Relationship between moonlight and father plumage colour and the effect on offspring body mass (predicted surface from a LMM). **b**, Detailed effects of moonlight on nestling body mass. Shown are the observed mean values of nestling body mass (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 224 observations, largest dots = 993 observations), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval for barn owls above the 3rd quantile (reddest owls) and 1st quantile (whitest owls) of colour variation. **c**, Relationship between moonlight (at nestling age of 15 d) and father plumage colour for fledging success of low-rank owlets (rank ≥ 7). **d**, Relationship between fledging success of low-rank owlets and moonlight (at nestling age of 15 d) raised by the whitest fathers (plumage colour ≤ 1st quantile) and the reddest fathers (plumage colour ≥ 3rd quantile). Lines indicate the regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval, and dots indicate the observed fledging success (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 8 observations).

Contrarily, food provisioning, hunting success and offspring body mass in the whitest owls were less or were not affected by moonlight (Figs. 2 and 4a,b). The whitest owls might actually perform better during full-moon nights, as suggested by the survival of their youngest nestlings raised being positively related to moonlight (Fig. 4c,d). In our population, the diet of both white and red owls is dominated by common voles, but white owls consume wood mice, *Apodemus* spp., more frequently than red owls[38]. However, differences in the diet associated with colouration are unlikely to drive the observed effects in our study because both *Apodemus* and *Microtus* show moon-avoidance behaviours[47–49].

Contrary to our expectations, plumage colouration did not affect the probability of voles detecting an owl (Fig. 3a). This suggests that white owls do not pay a higher cost of detectability than red owls (note that differences might still exist but went undetected in our study). However, there might be a benefit to white plumage in full-moon conditions as white plumage induces longer freezing times in rodents (Fig. 3b). Bright light is an aversive stimulus for rodents[50–53], and even small amounts of light (between 10^{-3} and 10^{-2} cm m^{-2} of luminance; that is, below the luminance of a full-moon night[23]) are aversive, at least in rats[54]. In fact, light is often used in neuroscientific studies to trigger freezing behaviour and to study the mechanisms of fear[55]. Given this fact, it is possible to interpret longer freezing times in voles attacked by a white owl as the result of a greater aversion to the light reflected by a white plumage. This is further supported by the lower freezing times that voles showed after masking the plumage reflectance of a white owl (Fig. 3c,d). This experiment showed that the amount of light reflected from the plumage was the factor influencing voles' freezing times.

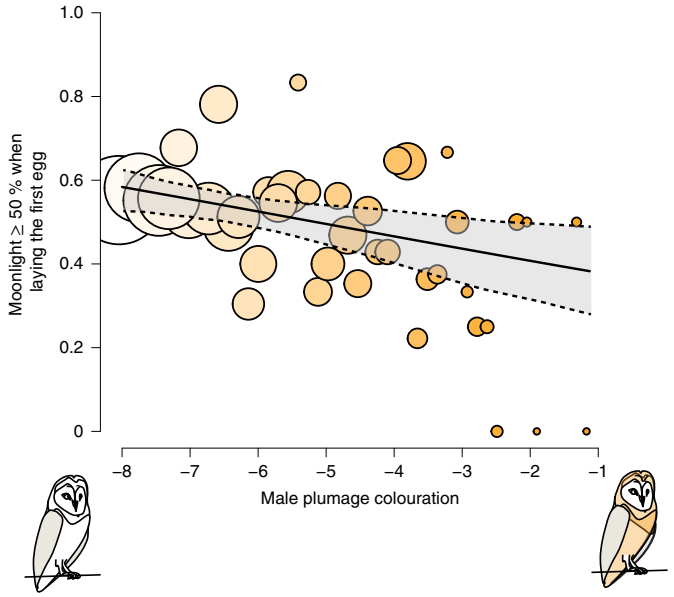

Fig. 5 | Plumage colouration in association with moonlight levels on the night females laid the first egg of a clutch. Probability that a female laid the first egg during nights with 50% or more of the Moon surface illuminated in relation to male plumage colouration. Shown are the observed proportions of cases (pooled every colour unit to the first decimal, smallest dots = 1, largest dots = 181), the regression line and the 95% confidence interval.

Inducing longer freezing times in prey can be adaptive for barn owls because a barn owl's hunting success substantially increases when prey stays immobile (up to 100% in laboratory conditions[43,44]). By exploiting sensory biases in the prey[56], white owls might enhance their hunting success during full-moon nights, explaining why moonlight had a smaller or no effect on food provisioning and hunting success of the whitest owls in comparison to the reddest owls. Whether the freezing responses of prey species others than common voles are also affected by the white barn owl plumage still needs to be assessed. Light aversion has been observed in mice of the genus *Mus* and in rats (*Rattus norvegicus*), so it is likely that other prey species common in the barn owl's diet, such as mice of the genus *Apodemus* (~20% of the barn owl's diet[38]), are also aversive to light and might respond to white and red plumage differently. Evidence supporting the notion that males make a larger hunting effort than females (this study) and are selected to have more immaculate plumages[57,58] suggests that a white colouration might have evolved by enhancing male hunting capacity.

Given the effect of moonlight, we would expect red males to be rare in our population. However, white colouration may incur costs that inhibit white males from becoming more frequent. White plumage might compromise camouflage during the day, particularly against harassing competitors, such as carrion crows (*Corvus corone*). There might also be added benefits of displaying a redder plumage, particularly under harsh conditions when a higher melanin content in feathers could increase protection against feather abrasion, humidity and/or cold temperatures[59]. Thus, the hunting-related benefits of white plumage may trade-off against survival to some extent. In this case, we expect white plumage to be less frequent in owls exerting lower hunting efforts, such as females and fledglings, which is in line with their, on average, redder plumage colouration[34,60,61]. We can then expect different selective agents inducing balancing selection on adult male colouration, which might maintain colour variation in this species, perhaps in combination with ontogenetic conflict within males and sexual antagonistic selection.

Small white patches are common among nocturnal species[9]. We predict that, as observed here, their ecological and evolutionary significance will be better understood when considering how their effect on fitness changes with varying moonlight levels. A question that remains open is whether selection exerted by moonlight is sufficiently strong to induce an evolutionary change in colouration. Here, we observed that moonlight acts on the total number of fledglings produced by males raising broods of at least seven owlets. This comprises 26.7% of the broods per year (Supplementary Fig. 3b), ranging from 8.3% to up to 48.5% depending on the year[62]. Thus, even though the fitness effect of the Moon is restricted to some individuals, it may affect a substantial part of the population and with particular strength in some years. Once they have fledged, the recruitment of nestlings in the local breeding population is not related to their rank in the brood (binomial GLMM: $\chi^2_1 = 0.37$, $P = 0.54$, mean recruitment: 15.73% ± 2.54), supporting the notion that the differences in the breeding success of red and white males generated by moonlight may persist after nestlings fledge and have evolutionary consequences. Nevertheless, we cannot yet discard that the high juvenile mortality (the major fitness component in our population[62]) finally hinders any evolutionary response to moonlight. Thus, studies integrating the effects that the Moon has inside and outside the breeding season are still needed to understand the evolutionary consequences of moonlight.

We observed that the Moon also influences breeding timing in barn owls of different plumage colouration (Fig. 5), suggesting that owls adjust their phenology to the Moon cycle. As observed in raptors exhibiting colour polymorphism[63], this effect is in line with owls having evolved mechanisms that minimize the negative impact of varying light conditions on their offspring. Thus, by laying their first egg during nights of lower moonlight levels, the period of maximal growth in the youngest nestlings of the reddest males will also occur during nights with low moonlight levels, which may help the reddest males to avoid the observed negative effects of high moonlight levels. Moonlight might also influence breeding timing because males might indirectly drive oviposition through courtship feeding[64]. Thus, the Moon might also determine the onset of reproduction by affecting the number of prey that males of different colouration offer during courtship. In line with this hypothesis, we observed that first in-nest copulations were also more likely to occur with higher and lower moonlight levels in the whitest and the reddest males, respectively. However, roughly 60% of the first in-nest copulations occur without courtship feeding in barn owls[45], suggesting that the Moon might have a smaller influence at this time.

In conclusion, our study shows that light variation associated with the Moon cycle exerts selection on the plumage colouration of a widespread nocturnal predator, the barn owl. Similar to the effect of varying diurnal light conditions[6,65], light variation during the night is also an important ecological factor in our understanding of the colouration of nocturnal species. Interestingly, our study provides evidence for the idea that white barn owls exploit sensory biases in their prey, which might enhance prey catchability and help white owls to buffer the negative effects of moonlight. In line with the increasing evidence supporting the existence of accurate colour vision in numerous nocturnal species[26,40], our study contributes the idea that colour is important in nocturnal systems. This raises the concern that light pollution has the potential to interfere with the evolutionary and ecological dynamics associated with colouration of nocturnal species, which deserves the attention of future studies.

Methods

Study site and species. The study area comprises 1,070 km^2 between the lakes of Neuchatel and Leman in western Switzerland. Since 1991, 360 nest-boxes installed

in farms were regularly monitored for barn-owl clutches. Eggs are laid every 2–3 d and incubation starts with the first egg, resulting in a marked age hierarchy (rank) among nestlings due to asynchronous hatching. The nests were revisited at least 4 times to capture the adults and record offspring development until fledging (rougly 55 d old). We used a balance to weigh owlets to the nearest 0.01 g, and their ages were estimated on the basis of wing length, measured to the nearest 1 mm, soon after their hatching. An individual was considered to have successfully fledged if it survived until the age of 55 d. Fresh prey remnants (number and species) were recorded on every visit to the nests. Prey remnants are those prey items that were not consumed by the nestlings and/or the females before our visit and therefore do not directly reflect total parental food provisioning.

Moonlight and colour measurements. The plumage colouration of adults was scored on the breast, belly, flank and the underside of the wings using an eight-colour chip ranging from −8 (white) to −1 (dark reddish), a method that highly correlates with objective spectrophotometric measurements of brown chroma (the ratio of long-wavelength reflectance, R600–700 nm, over total reflectance, R300–700 nm, see ref. [61] for further details). The average colour of all body parts was used for the statistical analyses. Barn owls also present a varying number of dark spots on their ventral plumage that are subject to sexual selection[66]. Including plumage spottiness on the models did not alter the results of the study (Supplementary Table 10).

Moonlight was measured as the visible percentage of the Moon. Except for the analyses on hunting success, we used the Moon visible percentage when the Moon passed the meridian as a single moonlight value for each night. The nights that moonset occurred within 1 h following sunset or that moonrise occurred within 1 h before sunrise (that is, the Moon was not visible during most of the night) were assigned a value of zero. The analysis of hunting success was based on observations at specific time points of the night, and hence we obtained values of the visible percentage of the Moon at each specific time point. For the analyses on offspring body mass, we collected data on moonlight of the night prior to the capture of the nestlings. For the analyses on offspring survival, we collected data on the moonlight levels at the nestling age of maximal growth rate (15 d old, mass gain 14.3 g d^{-1}, Supplementary Fig. 4), which is when nestlings are more sensitive to reduced food provisioning (nestlings that did not survive to fledging received less prey at age 15 d than those that survived; $t_{36} = -2.86$, $P = 0.007$). For the analyses on the association between moonlight and breeding, we collected data on moonlight for the night the females laid the first egg (assessed on the basis of the developmental stage of the clutch at the first time we visited the nest). We also collected data on moonlight for the nights when the first in-nest copulations were expected to occur (27 d before the first egg was laid[45]) and for the nights when nestlings of rank 6–8 were expected to reach an age of 15 d (given 14 d between the 1st and the 7th egg are laid, plus 31 d of incubation, and 15 d after hatching).

All the moonlight data were obtained for a locality within the study area (Yverdon-les-Bains; 46° 46′ 44′′ N, 6° 38′ 24′′ E) using a Javascript library (MeeusJs) developed by F. Soldati (www.github.com; last access in November 2018). The visible percentage of the Moon was square-root transformed for all the statistical analyses as this transformation improves the association with night illumination (Supplementary Fig. 1). Because nights with intense cloud cover are likely to introduce error in the effect of moonlight measured as the visible percentage of the Moon, we repeated the analyses including cloudiness as a predictor whenever possible. The models were re-run while considering cloudiness (percentage of the moon covered by clouds), which might affect light variation during the night. Including cloudiness in the models did not qualitatively change the results unless indicated otherwise in the Results section.

Parental food provisioning, GPS tracking and hunting success. Food provisioning was measured using infrared cameras at a total of 131 nest boxes ($n = 1{,}154$ observations of 201 different parents) in 5 years (1997, 2001, 2005, 2006, 2016). During the years 1997, 2001, 2005, and 2016, we used infrared video cameras (CCTV miniature cameras, Active Media Concept, France) connected to a recorder (Monacor International, Germany) and, in 2016, we equipped the nests with motion-sensitive camera traps (HC500 Hyperfire, RECONYX, USA). Food provisioning was recorded between 21.5 and 5.5 h for 3.4 nights ± 2.4 (s.d.) per nest on average. From the videos and pictures, we counted the total number of prey items brought on each night by the male and female parents, which were previously captured and ringed on different legs to facilitate their identification in the videos and pictures (for further details, see ref. [67]).

We monitored the foraging behaviour of 34 breeding male barn owls in 2016 and 45 in 2017 using GPS trackers. We used GiPSy-5 GPS tags (Technosmart, Italy) that measured 30 × 20 × 10 mm with the battery. These were coupled with a 40-mm-long antenna. The tags weighed between 12 and 13 grams (less than 5% of an owl's body mass) and were attached as a backpack with a Teflon harness. Each tag collected location, time and speed over ground every 10 sec at night, from 30 minutes before dusk to 30 minutes after dawn, to ensure a complete measurement of the activity period. In 2016 and 2017, breeding males were captured at their nest sites when the oldest nestling was 19–34 d old (mean = 25.4; s.d. = 2.8), equipped with GPS tags and released at the capture site. Approximately 2 weeks later, the owls were recaptured at the nest site in order to recover the GPS tags with the data. The trackers recorded the spatial location of each owl for an average of 8.1 nights ± 2.6 s.d. per owl. Prior to any analysis, GPS data were pre-processed and filtered for aberrant positions based on either speed or location.

An expectation-maximization binary clustering (EMbC) algorithm[68] was applied to classify barn owl movement data into different behaviours. EMbC uses an unsupervised approach (that is, based on no previous classification of the data) to cluster location data based on speed and turning angle between locations. We were interested in describing three main behaviours: perching, commuting and hunting. Perching was defined as a stationary behaviour, characterized by null or low speed and a wide range of turning angles due to the GPS error. Commuting was defined as a rapid straight flight, characterized by high speeds and low turning angles, often displayed after a prey capture between the hunting grounds and the nest box. Lastly, hunting was characterized by a slow and sinuous flight, with low to medium speed and medium to high turning angles. For validation, the EMbC behavioural classification was compared with a visual classification performed on a random subsample of the whole dataset (20 individuals). The correspondence between EMbC and the visual classification was high: 92.7% on average (perching = 94.5% ± 2.3 s.e.; commuting = 91.1% ± 3.8 s.e.; hunting = 92.6% ± 4.9 s.e.). Therefore, we considered EMbC's classification as reliable.

After detecting each event when the owls were likely to be hunting ($n = 13{,}558$), we classified a hunting event as successful if the owl flew back to its nest immediately afterwards (that is, it commuted) or as unsuccessful, if the owl resumed hunting. Although this indirect measure of hunting success might include as successful those cases when males visit the nest without a prey item and might leave out cases when an owl hunts close to and from a perching site, we found a good correspondence between the mean prey delivery rate of males per night observed using infrared cameras (7.08 preys ± 3.52 s.d.) with that estimated using the GPS tracks (8.94 preys ± 5.31 s.d., exact Poisson test $P = 0.45$). Additionally, the observed mean hunting success (~0.41 ± 0.1 s.e.) is also within the range observed in a previous study measuring owl success in catching prey in captivity (0.42 ± 0.2 s.e.)[44]. Thus, we consider that our indirect measurement of success is a good proxy for real hunting success.

Behavioural experiments. We used common voles, *Microtus arvalis*, to investigate how prey react to barn owls of different plumage colouration and under different light conditions. Common voles are the staple prey in our owl population (~55% of the diet[38]), and the analysis of fresh vole remains found in the nests suggests that the number of voles that owls capture depends on the interaction between moonlight and the owls' colouration in the same way as described above for food provisioning ($z = 2.11$, $P = 0.035$; fewer voles as prey remains the day after a full-moon night than after a new-moon night in the reddest owls: $z = -1.98$, $P = 0.048$; no effect of Moon cycle on the number of voles as prey remains within the whitest owls: $z = 1.46$, $P = 0.143$, Supplementary Table 11 and Supplementary Fig. 5).

The voles were captured within the first 2 weeks of February 2015 ($n = 24$) and on the first 2 weeks of March 2016 ($n = 23$) using Longworth live traps in the surroundings of the University of Lausanne, Switzerland and were housed individually in plastic terraria (42.5 × 26.6 × 18.5 cm) at the animal facilities of the University of Lausanne, Switzerland. The room temperature and humidity were kept constant at 22 ± 1 °C and 50%, respectively. Food (rodent food pellets, seeds and apple pieces) and water were provided ad libitum. The terraria were equipped with a hiding place, and hay and sawdust served as the substrate. We left the voles to acclimate to the laboratory conditions for 10 d and recorded their behaviour to the different owl colour morphs and light conditions during days 11 and 12. On day 13, they were released at the exact location where they were captured.

On the night of day 11, the voles were moved to a dark room enclosed by black cloth (Supplementary Fig. 6a) and placed individually in a larger terrarium (80 × 35 × 40 cm) with new substrate mixed with a handful of the substrate from the rodent terrarium to minimize stress. The room was divided into three lines (2.80 m large, 2 m high and 1 m wide) by black cloths, and two terraria were placed at the end of each line (the sides of the terraria were covered with black paper to keep the voles from seeing each other). To measure the vole response to owl colour morphs, we used two white (plumage colour score of −8) and two red (plumage colour score of −2 and −3.25) owls that were taxidermized in a flying posture (Supplementary Fig. 6c). The owls were suspended 1.60 m above the ground with a transparent nylon string and remained hidden under a black cloth at the end of each line at the opposite end of the voles' terraria. Twenty minutes after the voles were placed in the large terraria, we opened the cloth hiding the owl and let the owl slide through a 2-m-long zipline that went down to the opposite end of the line, which is where the voles' terraria were placed (Supplementary Fig. 6b). The 2-m length of the zip-line was chosen because the antipredatory response of the only rodent species previously tested (the spiny mouse, *Acomys cahirinus*) against an attacking barn owl occurred mainly within a range of 0–2 m between the owl and the rodents[44]. The owls were moved backwards along the zip-line and released again 2 more times (which were separated by 5 minutes), simulating the multiple attacks that owls often perform on their prey[43,44].

For each vole, the same procedure was repeated after 1 h on the same night but with an owl of a different colour. On the following night, the procedure was repeated with a different light condition (that is, at the end of the experiment, each

vole was exposed to owls of both colourations and under both light conditions). To mimic full-moon light conditions, we placed two halogen lights (470 lumen each) attached together in one side of the room and at a distance of 3 m (Supplementary Fig. 6b). Halogen lights have been successfully used in previous studies to trigger moon-dependent behaviours[14], given their spectral similarity to the moonlight[69,70]. The light source was separated from the rodents by several black cloths so that the light in the first line measured with a standard luxometer was 0.25 lux, equivalent to full-moon light conditions at temperate latitudes[71]. To mimic new-moon conditions, the halogen lights were turned off, resulting in values below the detection level of the luxometer (<0.001 lux). The order with which the treatment (that is, the colour of the taxidermized owl) and the light conditions were applied to each rodent were randomized but controlling that there were the same number of trials for each combination of treatment order and light conditions.

In 2016, we included an additional manipulation to test whether the effect observed on the voles' freezing times was dependent on the amount of light reflected from the owls' white plumage. We exposed the rodents to a white owl, also taxidermized in a flying posture and whose plumage colouration was treated with duck preen wax ('cul de canard', CDC, Petitjean Fishing Equipment, SA, Switzerland) in addition to the red and white owls used in 2015. CDC was gently applied with a brush (6 drops per cm^2 of plumage) and significantly decreased plumage reflectance within the ultraviolet and visible wavelength ranges (see Fig. 3c).

During the trials, vole behaviour was recorded with two infrared video cameras, one located within the terraria and another located in a position above the terraria. From the video footage, we determined whether the voles responded to the owls (by either freezing or fleeing) or not (that is, the voles' behaviour remained unaltered after owl presentation). The amount of time that each vole spent frozen (time between the voles froze and resumed their activity) was measured from the videos to the nearest second. Because we were interested in investigating the response of the voles in relation to owl colouration, all the observations where the voles' orientation made them unable to see the owls were excluded (49 % of the trials). The final mean number of observations per vole was 6.04 ± 2.23 (s.d.) and was not significantly related to the owl colouration, the light conditions or the repeated exposure to the owls (all $t_{23} < 0.97$, $P > 0.34$).

Statistical analyses. All statistical analyses were conducted with R 3.0.2 (R Core Team, Vienna, Austria). LMMs and GLMMs were fitted with the functions lmer and glmer, respectively, implemented in the package 'lme4'[72]. GLMMs on food provisioning as a Poisson response variable included the random effect of Parent ID to account for repeated measurements on the same parents over several nights, Brood ID to account for male and female parents provisioning the same brood and Year ID to account for interannual variability in prey abundance. Fixed factors included moonlight, plumage colouration of the parent and their interaction. The fixed effects of sex, brood size and their interaction, and egg-laying date (including quadratic effects to account for within-year variation in prey abundance) were also included. GLMMs on hunting success as a binomial response variable included the random effects of Male ID to account for repeated measurements taken on the same male over several nights, and of Night ID (nested in Male ID) to account for repeated measurements on the same male within the same night. Year was included as a fixed factor given that the study only covers two years of GPS tracking. Fixed factors included moonlight at the beginning of a hunting event, male plumage colouration, hunting effort (the number of times a male was observed hunting over a given night) and all two-way and the three-way interaction between these terms. Hunting effort was included in the models because it may affect hunting success owing to owl's fatigue when hunting many times over the same night or because effort can reflect how suitable the conditions for hunting were over a given night (for example, low efforts might reflect poor climatologic conditions). We considered hunting effort in interaction with plumage colouration (and moonlight) because plumage colouration might associate with differences in stamina[73] and with different tail and wing morphologies that might affect how red and white owls hunt under different conditions[74]. We also included the linear, quadratic and cubic effects of the time of each hunting observation, after visually detecting that hunting success strongly decays during dawn and dusk. As for the models on food provisioning, the fixed effects of brood size and the linear and quadratic effects of laying date were also included.

The statistical models on vole behaviour (GLMM on vole probability to detect an owl as a binary response and LMM on freezing time) included the random effects of vole ID to account for repeated measurements on voles (each vole faced the same treatment three consecutive times), session (each vole was tested in the two moonlight conditions and with the two owl morphs), lane to account for potential variation within the experimental room and block (each year, voles were captured and tested in the experimental setting in groups of 7–8 voles). Fixed effects included owl morph (red versus white), moonlight condition (full- versus new-moon) and their interaction. The fixed effect of year (two-levels factor) and its interaction with the other terms was included to account for the fact that the experiment was repeated in two separate years by different observers. Repetition was included to account for differences in the response between the first, second and third time the same owl was presented to the rodents. For the analysis of time spent frozen, mean times of the three repetitions were taken.

LMMs on nestling body mass (log-transformed) were conducted on a total of 18,735 records of offspring body mass collected for 3,878 nestlings born over the last 20 years in 814 different broods. The models included the random effects of owlet ID to account for repeated measurements of body mass on the same nestlings, including the random slopes for nestling age, age^2, age^3. The IDs of the brood in which nestlings were born and raised were included to account for the shared environment and origin of nestlings. The IDs of the foster parents were included to account for repeated breeding of the same parents across several years. Fixed effects included moonlight, father plumage colouration and their interaction, as well as the following factors, which are known to affect nestling body mass: age (up to the fourth power[75]), hour (up to the third power), laying date (linear and quadratic), brood size and rank within the brood hierarchy. We only considered the colouration of the father given the larger male hunting effort. Males alone feed both their offspring and female partners until the first-born owlet is 2–3 weeks old[46]. From this time onward, females leave to produce another clutch[76] or stay but hunt significantly less than males (the average number of prey per night for females was 3.79 ± 0.67 (mean ± s.e.) versus 7.08 ± 1.21 for males; $z = 9.38$, $P < 0.001$, Supplementary Table 1).

GLMMs on nestling survival as a binary response variable included the same random and fixed terms as for models on nestling body mass except for owlet ID (no replication in survival within individuals), age and hour. These models were conducted on data from 4,504 nestlings from 944 broods monitored in the last 20 years, whereas the analyses restricted to nestlings of rank ≥7 was conducted on 217 barn owl nestlings from 150 broods. The GLM initial full model on the survival of nestling of rank ≥7 show evidences of underdispersion, and we used a penalized likelihood approach (function glmmPQL, package 'MASS')[77].

To test for an association between male colouration and moonlight levels on the date females laid their first egg ($n = 1,293$ clutches raised by 631 different males between 1994 and 2017), we created a binomial variable considering whether moonlight was ≥50% or <50% on a given date. We then fit a GLMM with moonlight as a binary response and considered the random effects of Year and Male ID (to account for repeated observations on the same males), and the fixed effect of male colouration. The same approach was used but with consideration of moonlight levels on the date when the first in-nest copulations were expected to occur and on the date when a females' nestlings of rank 6 or more were expected to reach the age of 15 d old.

For all models, Cook's D values were computed from the models to assess the influence of the observations on model performance, and collinearity was assessed by calculating the variance inflation factor for each of the quantitative parameters in the models[77]. All full models were simplified by backward elimination of non-significant terms ($P > 0.1$), which provided qualitatively similar results as when using an information-based (AIC) approach[78] (Supplementary Table 12). For posterior contrasts on the interactions between colour and moonlight, we performed multiple 'simple slopes tests'[77] using the minimum and maximum values of colour and moonlight as conditional values. The P values from the contrast tests were adjusted to account for multiple testing using the Benjamini–Hochberg approach. Significance was set at 0.05 (two-tailed).

Ethics. The monitoring of barn owls was performed under the legal authorization of the 'Service vétérinaire du canton de Vaud', Switzerland. Barn owls were equipped with GPS devices under the authorization of the 'Service vétérinaire du canton de Vaud', Switzerland (Authorization VD2844.a and VD3213). The voles were captured under the permit 2154 of the Canton de Vaud, Switzerland, and the behavioural experiments were authorized by the 'Service vétérinaire du canton de Vaud', Switzerland (Authorization VD2934).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available from the corresponding authors upon reasonable request. The GPS data used to assess hunting success is stored in Movebank (www.movebank.org) and accessible under the project named 'Barn owl (*Tyto alba*)' (Movebank ID 231741797).

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Author contributions

A.R., A.A. and L.M.S.-J. conceived and designed the study. A.R., P.B., B.A., R.S., K.S. and C.G. collected the field data on barn owls. R.S., K.S. and C.G. conducted the GPS-tracking study with contributions from P.B. and B.A. L.M.S.-J., C.J., A.Q. and A.O.-X. designed and conducted the behavioural experiments with voles. L.M.S.-J. conducted the statistical analysis with the contribution of R.S. L.M.S.-J. and A.R. wrote the paper, with major contributions from A.R., A.K., and R.S. and with input from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Information about moonlight was obtained using a Javascript library (MeeusJs, Fabio Soldati, www.github.com, last access on May 2018)
Data analysis	R 3.0.2

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The GPS data is accessible at Movebank (www.movebank.org, Movebank ID 231741797). The rest of the data set is available from the corresponding authors upon reasonable request.

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☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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All studies must disclose on these points even when the disclosure is negative.

Study description	The study is both experimental and correlative. The correlative part is divided into 5 sections to study i. food provisioning of (male and female) adults (Observations = 1154, taken on 201 different adults from 131 nests), ii. hunting success in adult males (Observations = 13558 on 79 males followed on average across 8.07 nights, 2.65 S.D.), iii. nestling body mass (Observations = 18735 on 3878 nestlings from 814 different nests), iv. nestling survival (records on 4504 nestlings from 944 broods, 217 nestling from 150 broods for the analysis restricted to the youngest nestlings), v. moonlight levels during egg laying (1,293 clutches of 631 males). For all this sections, the main predictors were moonlight (% of the Moon visible) and adult (both male and female) plumage coloration (i) and parent plumage coloration (ii) and the interaction between moonlight and plumage coloration. For v., only male plumage coloration was considered as the main predictor. The data of all these sections is hierarchical to a different extent depending on the analysis, as described in the tables of the supplementary material and in the methods section. The experimental part of the study was conducted following a repeated-measures design where factor levels (Moonlight and Owl coloration) were applied up to 3 times and following a crossed design to all the experimental units (47 common voles).
Research sample	The research sample for the correlative part is from a population of adult and nestling barn owls, Tyto alba, breeding in nest boxes in Western Switzerland. The sample size is determined by the number of breeding couples encountered each year. For the experimental part, we sample common voles, Microtus arvalis, inhabiting the surroundings of the campus of the University of Lausanne, Switzerland. The sample size for this part was determined after a preliminary power study.
Sampling strategy	Barn owls were sampling by visiting the nest boxes periodically during the breeding season. Sample sizes involving barn owls were determined by the number of breeding couples present in a year. A post-hoc power analysis (based on 1000 simulations of the dependent variable based on final model estimates, "simulate" function in R v.3.0.2, package lme4) indicates that power to detect the reported effects given the sample size was > 0.80. Voles were captured using traps placed at different sites of the campus of the University of Lausanne, Switzerland. The sample size for this part was determined after a preliminary power study using the "pwr" package of R v.3.0.2.
Data collection	Data on plumage colouration of adults was scored using an eight-colour chip ranging from -8 (white) to -1 (dark reddish), a method that highly correlates with objective spectrophotometric measurements. Depending on the year, it was recorded by Alexandre Roulin, Robin Sechaud, Paul Bezier or Betina Almasi. Data on the moonlight was obtained by Luis M. San-Jose for a locality within the study area (Yverdon-les-Bains; 46°46'44'' N, 6° 38'24'' E) using a Javascript library (MeeusJs) developed by Fabio Soldati (www.github.com, last access on May 2018). Data on food provisioning was measured by Alexandre Roulin, Robin Sechaud, and Betina Almasi using sensitive infrared video cameras (years 1997, 2001, 2005, and 2016) or camera traps (2016). Data on hunting success was measured from GPS location data using GiPSy-5 GPS tags mounted on the owls by Robin Sechaud, Kim Schalcher, and Charlène Gémard. The data was processed by Robin Sechaud using an Expectation-Maximization binary Clustering. Data on nestling body mass (measured using a balance to the nearest 0.01 g) and survival before fledging was obtained by Alexandre Roulin, Robin Sechaud, Paul Bezier and Betina Almasi. Data on vole antipredatory response was obtained by Luis M. San-Jose from the footage recorded by two infrared video cameras, one located within the terrarium of each rodent and another located in a position above the terrarium of each rodent.
Timing and spatial scale	Data on plumage coloration, nestling body mass and survival has been continuously recorded since 1991 during the breeding period (February-October). Food provisioning was monitored during the years 1997, 2001, 2005 and 2016 as part of different studies. Hunting success was recorded during 2016 and 2017. Rodent behavior was experimentally tested during the years 2015 and 2016. The spatial scale is local (Western Switzerland for barn owl data, campus of the University of Lausanne for the vole data).
Data exclusions	No observations were excluded expect for the experimental study. As we indicate in the methods:"Because we were interested in investigating the response of the voles in relation to owl coloration, all the observations where the voles' orientation made them unable to see the owls were excluded (49 % of the trials)."
Reproducibility	The rodent experiment was conducted on two separate years with the same findings (Year has no interactive effect with the experimental factors, see Supplementary Table 4).
Randomization	Randomization was applied to allocate the order of the treatments (moon condition and owl coloration) to the voles (all the treatments were applied to all the voles).
Blinding	Most of the data was collected before starting this study and was therefore blind to Moon conditions. Data collection from the videos of the experiment with voles could not be done blindly in relation to the Moon conditions as this is visible on the videos. However, this data was collected blindly in relation to the plumage coloration of the stuffed owls. No blinding was used during the data analysis.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Not recorded

Location	The study area comprises 1,070 km2 between the lakes of Neuchatel and Leman in Western Switzerland.
Access and import/export	All the authorizations to capture and manipulate the animals used in the study were given by the 'Service vétérinaire du canton de Vaud' (Switzerland). All the pertinent permits are reported in the Methods section.
Disturbance	To the best of our knowledge, the study cause no mayor disturbances on the barn owls or the voles. We minimize the duration of the visits to the owls' nests, the size of the GPS tags, and the number of days the voles were kept in the laboratory.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Adult and nestling barn owls, Tyto alba, of both sexes, that were captured in nest boxes either by hand or with the help of a net at the entrance of the nest. The owls were not transported to the laboratory but released in their nest immediately after manipulating them. Adult common voles, Microtus arvalis, of both sexes were caught in the field using traps and released in the location they were captured after the experiments.
Field-collected samples	The study did not involve samples collected on the field.
Ethics oversight	Veterinary service of the Canton of Vaud, Switzerland.

Note that full information on the approval of the study protocol must also be provided in the manuscript.