



SYMPOSIUM ARTICLE

Evolutionary and Ecological Correlates of Quiet Flight in Nightbirds, Hawks, Falcons, and Owls

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Synopsis Two hypotheses have been proposed for the evolution of structures that reduce flight sounds in birds. According to the stealth hypothesis, flying quietly reduces the ability of other animals (e.g., prey) to detect the animal's approach from its flight sounds. This hypothesis predicts that animals hunting prey with acute hearing evolve silencing features. The self-masking hypothesis posits that reduced flight sounds permit the animal itself to hear better (such as the sounds of its prey, or its own echolocation calls) during flight. This hypothesis predicts that quieting features evolve in predators that hunt by ear, or in species that echolocate. Owls, certain hawks, and nightbirds (nocturnal *Caprimulgiformes*) have convergently evolved a sound-reducing feature: a velvety coating on the dorsal surface of wing and tail feathers. Here we document a fourth independent origin of the velvet, in the American kestrel (*Falco sparverius*). Among these four clades (hawks, falcons, nightbirds, and owls), the velvet is longer and better developed in wing and tail regions prone to rubbing with neighboring feathers, apparently to reduce broadband frictional noise produced by rubbing of adjacent feathers. We tested whether stealth or self-masking better predicted which species evolved the velvet. There was no support of echolocation as a driver of the velvet: oilbird (*Steatornis caripensis*) and glossy swiftlet (*Collocalia esculenta*) each evolved echolocation but neither had any velvet. A phylogenetic least squares fit of stealth and self-masking (to better hear prey sounds) provided support for both hypotheses. Some nightbirds (nightjars, potoos, and owlet-nightjars) eat flying insects that do not make much sound, implying the velvet permits stealthy approach of flying insects. One nightbird clade, frogmouths (*Podargus*) have more extensive velvet than other nightbirds and may hunt terrestrial prey by ear, in support of self-masking. In hawks, the velvet is also best developed in species known or suspected to hunt by ear (harriers and kites), supporting the self-masking hypothesis, but velvet is also present in reduced form in hawk species not known to hunt by ear, in support of the stealth hypothesis. American kestrel is not known to hunt by ear, and unlike the other falcons sampled, flies slowly (kite-like) when hunting. Thus the presence of velvet in it supports the stealth hypothesis. All owls sampled ($n = 13$ species) had extensive velvet, including the buffy fish-owl (*Ketupa ketupu*), contrary to literature claims that fish-owls had lost the velvet. Collectively, there is support for both the self-masking and stealth hypotheses for the evolution of dorsal velvet in birds.

Introduction

Why have certain birds evolved “silent” flight (by “silent,” we actually mean quiet flight)? One or more of four possible types of receivers: self, predators, prey, or conspecifics, has selected for an animal to reduce the acoustic signature it produces in flight. Sounds of flight may mask the animal's own ability

to hear salient sounds (such as prey sounds) during flight. Thus, under self-masking, quiet flight may have evolved to reduce the degree to which the animal's wing noises interfere with (i.e., mask) its own ability to hear (Clark et al. 2020). The other three receiver types are other animals: predators (including parasites), prey, or other animals (especially

conspicuous). Under the stealth hypothesis, ameliorating wing sounds reduces the focal animal's detectability to other animals, including its prey, predators (and parasites), or to conspecifics (Clark et al. 2020).

Owls are the bird clade best-known for quiet flight. One way that owls reduce their acoustic flight signature is through derived morphological features of their wing feathers (Graham 1934). These wing features include a morphological specialization of the leading edge of part of the wing, the comb; a fringed feather margin (Bachmann et al. 2007; Bachmann et al. 2012b); increased porosity (Müller and Patone 1998; Geyer et al. 2014), and slightly reduced flexural stiffness of their feathers (Bachmann et al. 2012a). Finally, there is the subject of the present study: the dorsal surface of flight feathers of many owl species has small (micrometer to millimeter scale) elongate filamentous projections, termed pennulae, which extend from each distal barble and collectively form a soft, velvety dorsal surface. Here, we explore the question: which birds have evolved the velvet, and what are the ecological correlates of this wing feature?

Prior research on quiet flight has focused almost exclusively on owls, but owls are not unique in possessing adaptations that apparently reduce their acoustic flight signature. Some, perhaps many Nightbirds (a grade within clade Strisores that does not include the diurnal Apodiformes) are reported to have both the velvet and fringed vanes on at least some primaries and secondaries (Lucas and Stettenheim 1972). Harriers (*Circus* spp.) and kites (*Elanus* spp.) also have the velvet on their primary feathers (Negro et al. 2006). Rice (1982) showed that harriers have can localize vole sounds played from a speaker, and at least one kite, the nocturnal letter-winged kite (*Elanus scriptus*) is reported to have asymmetrical ears (Negro et al. 2006). Ear asymmetry is significant because this is the ear morphology that allows some owls, such as Northern Saw-whet Owls (*Aegolius acadicus*) to discriminate azimuth from elevation from sound alone (de Koning et al. 2020; Beatini et al. 2018). Thus, asymmetrical ears imply an ability to use sound to localize prey.

Stealth

In the context of a stealthy predator, Clark et al. (2020) suggested that selection for stealth is a function of five variables: the wing sounds the predator produces; the attenuation of these sounds by the environment as they travel from predator to prey; background sound levels; any sounds the prey makes (that masks its own hearing); and the hearing ability

of the prey. How certain prey species use hearing to avoid predators has been particularly well-studied in flying insects (e.g., moths and beetles) and rodents. Flying insects are well-known to detect echolocating bats acoustically (Conner and Corcoran 2012; Strauß and Stumpner 2015). In theory, they could use wing sounds of birds to do the same (Jacobs et al. 2008; Fournier et al. 2013). Moreover, some rodents use sound to evade owls (Webster 1962; Ilany and Eilam 2008). For the purposes of this study, we only consider stealth of predators that eat prey that use sound to evade predators (i.e., of the four possible receivers named above, we ignore stealth relative to conspecifics or stealth from predators, since no studies of quiet flight have identified these receivers as a source of selection for quiet flight).

Self-masking

In the context of a predator that hunts by listening for prey, Clark et al. (2020) suggested that selection for self-masking is a function of five variables: the wing sounds the predator produces; the sounds the prey makes; the attenuation of these sounds by the environment as they travel from prey to predator; background sound levels, and the ability of the predator to hear the prey sounds. This argument can be modified slightly to account for other types of self masking, such as echolocation. In particular, swiftlets (*Collocalia* spp.) and oilbird (*Steatornis caripensis*) are closely related to other *Caprimulgiformes* that have evolved quiet flight. Each of these species has separately evolved the use of echolocation while flying in caves (Brinkløv et al. 2013), thus one sub-hypothesis we considered was that silencing features might be present in echolocating species to reduce self-masking during echolocation. More generally, for the purposes of this article, self-masking is predicted in birds that listen for sounds while hunting.

Here, we assess whether stealth or self-masking better predicts the evolution of the velvet. We first scanning electron microscopy (SEM)-imaged the proximal part of P10 of a variety of bird species, and developed a simple scoring system for presence of the velvet. We then visually assessed the presence of velvet on 10 points across the wing of 50 species of bird, primarily using specimens of spread wings from the Burke Museum. We focused on owls, hawks, nightbirds, and, as the SEM images indicated American kestrel (*Falco sparverius*) also had the velvet, falcons. Finally, we conducted phylogenetic statistics to assess whether masking or stealth were better predictors of the evolution of the velvet.

Methods

Environmental SEM of outer primaries

The outermost primary feather (P10) of 18 bird species were obtained from several sources, including whole animals or individual molted feathers salvaged in California under a California Department of Fish and Wildlife permit (#SC-006598) and a United States Fish and Wildlife Service Scientific Collecting permit (MB087454-0). P10 from a white-tailed kite (*E. leucurus*) was pulled from a skin in the University of California Riverside (UCR) vertebrate teaching collection. Outer primaries of Andean Condor (*Vultur gryphus*) were obtained from the Yale Peabody Museum, and molted Trumpeter Swan feathers (*Cygnus buccinator*) from the Livingston Ripley Waterfowl Conservancy (lrwc.net). From each feather, we selected a small portion of the trailing vane in a proximal region of each feather (i.e., corresponding to a region of the feather that is virtually always underneath and in contact with the vane of the proximal adjacent feather, P9). This section was subjected to environmental SEM (eSEM) using a Hitachi TM-1000 tabletop eSEM at the Institute for Integrative Genome Biology at UC Riverside. The feather samples were not treated prior to imaging.

The eSEM images were measured in the program ImageJ version 1.46r (Schneider et al. 2012). We measured the elongated portion of the pennulum (p in Fig. 1) on three distal barbules, taken as the linear distance from the distal end of hooklets to the tip of the pennulum. Some specimens showed signs of damaged or worn pennulae, for example, Western Gull (*Larus occidentalis*) feathers, which had been molted (i.e., they were old) and White-crowned Sparrow (*Zonotrichia leucophrys*) feathers appeared damaged as well. In these cases, we selected the longest pennulae available. This distance p is not the full length of the pennulum as defined by Lucas and Stettenheim (1972), since the entire pennulum also includes the region with hooklets that attach the distal barbule to the adjacent proximal barbules. This measurement, p , of the elongated portion of the pennulum was instead functionally relevant to the development of the velvet specifically, since it is the elongation of the pennulum beyond the hooklets that produces the velvet. Since feather size also varied by more than an order of magnitude, from the 5 cm P10 of White-crowned Sparrow to the >50 cm P10 of Andean Condor (*V. gryphus*), we controlled for size by calculating the pennulum to barbule ratio, p/b .

These eSEM images revealed continuous variation in elongation of the pennulum. From these images,

we developed a simple categorization of the degree to which the pennulae covered the top surface of a feather. A p/b ratio of 2 was the length at which the pennulae are long enough to form a complete covering (a monolayer) of the top surface of the feather. A $p/b > 2$ was a score of 2; $1 < p/b < 2$ received a score of 1, meaning that the surface of the feather was more than half covered by elongated pennulae; and $p/b < 1$ was assigned a score of 0, and corresponded to feathers that were less than half covered in pennulae. Among the feathers sampled, most species had p/b of >2 or <1 (Fig. 1), meaning that on this 3-point scale, most feathers scored either a 0 or a 2.

Distribution of velvet across the wing

We then visually scored the distribution of velvet across the wing for 50 species of bird, including a series of hawks and relatives (*Accipiteriformes*), owls (*Strigiformes*), nightbirds (*Caprimulgiformes*), and Falcons (*Falconiformes*), a shrike (*Passeriformes*; shrikes have independently evolved carnivory), as well as birds from several other orders. For 48 of these species, we examined spread wings ($n=1$ wing per species), primarily specimens at the Burke Museum (hereafter BM), and a few salvage specimens at UCR. For two species, spread wings were not available, and we instead examined a museum skin of an oilbird at the Museum of Vertebrate Zoology (MVZ # 123691), and a great potoo (*Nyctibius grandis*) skin (BM 76227).

On each spread wing specimen, we assessed the degree of development of the velvet on 10 dorsal locations on the wing and tail, under a dissecting scope (20 \times magnification, in most cases). We assessed five individual feathers: P10, P5, P1, S4, and the largest alula feather (Fig. 2A). On each feather, we measured two locations: a region exposed to airflow when the wing is spread (near the tip of the feather); and a covered region that is overlain by an adjacent feather when the wing is spread (e.g., closer to the base of the feather, on the trailing edge). To assess the covered region, the overlaying wing feather(s) on the specimen were gently pulled back to expose the normally-covered portion of the feather we sampled. A subset of species also had the dorsal surface of tail visually inspected under a dissecting scope to document presence of velvet. As only the innermost tail-feather (R1) is easily accessible on a typical museum skin, we were unable to systematically survey for the velvet on the tail. On the oilbird and great potoo skins, since the wings were not spread, only the tail and the outer

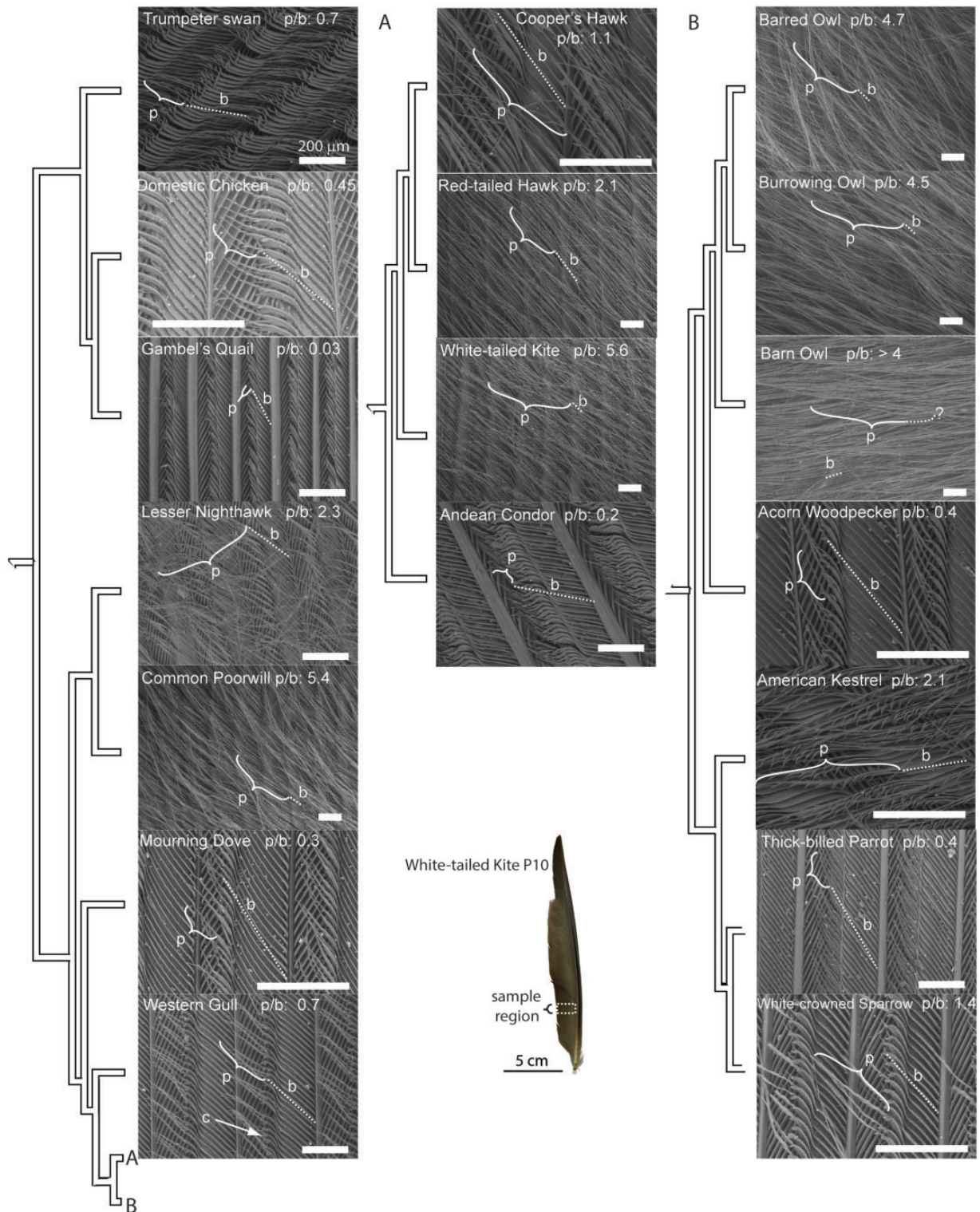


Fig. 1 eSEM images of the dorsal surface of the proximal vane of an outer primary of 18 species of bird, showing pennulae length (p) relative to the length of the distal barbule (b). Some species show “fastening barbules” or cilia (c) (Matloff et al. 2020). Phylogeny from Prum et al. (2015).

primaries were assessed. For statistics, the amount of velvet a species had was simply the average of the velvet scores for each of the 10 locations, yielding a

single number that varied between 0 (no location had a velvet score greater than 0) and 2.0 (every location examined had a velvet score of 2).

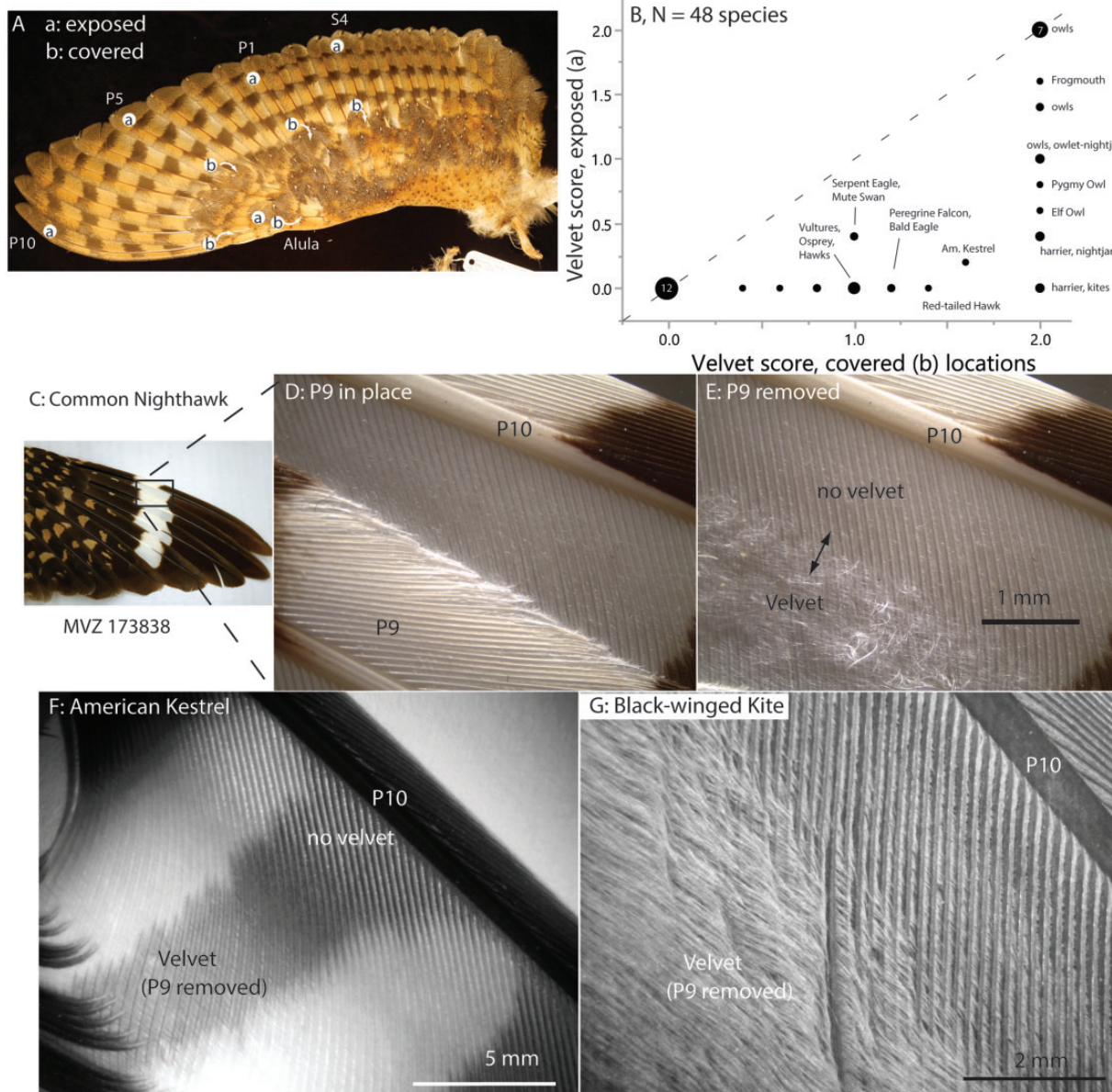


Fig. 2 Velvet tended to be longer in areas where wing feathers overlap than in locations exposed to the boundary layer. **(A)** Sample locations for measuring the presence of velvet, showing exposed (a), and covered (b) locations. In each case, for the covered sample locations, the adjacent overlaying feather(s) were gently lifted to expose the measurement location. Pictured: barn owl (*Tyto alba*) wing. **(B)** Average velvet score of covered (“b”) against exposed (“a”) locations, for 48 species. Dashed line is 1:1; no species fell above the line. Dot size proportional to number of species with that score. **(C)** Wing of common nighthawk (*Chordeiles minor*, a nightjar within Nightbirds). **(D)** Dorsal surface of P10 that is exposed to airflow has minimal velvet. **(E)** P10 in the region that is underneath P9 has extensive velvet. **(F, G)** American kestrel (BM 32499) and black-winged kite (BM 66216) show the same pattern (P9 has been lifted away to show covered region in each).

Ecological traits

Based on literature accounts of the natural history of each species, species were assigned a binary score (0 or 1) for whether quiet flight was selected for under either the stealth or self-masking hypotheses. Stealth was scored as follows: species that are predatory on flying insects at night (i.e., moths, beetles, and other insects that are caught on the wing), or are predatory

on rodents, were given a score of 1; all other species were given a score of 0. For self-masking, species that are known or suspected to listen for prey sounds while hunting were given a score of 1, while all other species were given a score of zero. Specifically, species hunting functionally silent prey, such as flying insects (e.g., most nightbirds) were assigned a score of zero. Species reported to have asymmetrical ears, such as many owls, but also, kites (Negro et al.

2006), or reported to locate prey by acoustic means alone, such as many owls, but also harriers (Rice 1982) and frogmouths (Kaplan 2018) were given a self-masking score of 1. Finally, species known to use echolocation were scored (1: echolocation present, 0: echolocation absent), since self-masking of echolocation calls by the wings might occur as well.

Phylogenetic statistics

A phylogeny was assembled from the Prum et al. (2015) phylogeny, supplemented with phylogenies of hawks (Mindell et al. 2018) and owls (Wink et al. 2009). Branch lengths were set in Mesquite version 3.6 (Maddison and Maddison 2015) using Pagel's arbitrary method. To test the masking and stealth hypotheses against each other, we used the *ape*, *nlme*, and *geiger* libraries in R version 3.4.1 (Paradis and Schliep 2019). We computed a phylogenetic generalized least squares (pgls) fit first assuming a variance-covariance structure of Brownian motion (i.e., Pagel's $\lambda = 1$), with velvet score (continuous variable between 0 and 2) as the dependent variable, and stealth score and masking score as the two binary independent variables. We then ran a second statistical model using the *corPagel* function in *ape*, which fits a value of λ to the data (rather than assuming $\lambda = 1$).

Results

eSEM images of the inner vane of P10 for 18 species are shown in Fig. 1. Among these 18 species, pennulum length varied from $6\ \mu\text{m}$ in Gambel's Quail (*Callipepla gambelii*) to $>1\ \text{mm}$ in barn owl, in which total length could not be ascertained because the pennulae are so thick they obscured the location of the base of the pennulum. There were two breaks in the distribution of this trait: 10 species had p/b ratios of <1.5 , three species had p/b ratios of roughly 2, and five species (three owls, white-tailed kite, and common poorwill) had p/b ratios >5 . In addition to species previously reported to have the velvet, the American kestrel (*F. sparverius*) P10 had extensive velvet.

Velvet distribution across wings of 50 species

Raw data and specimens examined are provided in Supplementary Table S1. Data for two species (oilbird and great potoo) were derived from museum skins. There was no velvet on the tail or any wing feathers sampled on the oilbird, thus we assigned it a velvet score of 0.0. On the great potoo, there was some velvet on its tail-feathers and some velvet present on the wing-feathers that were visible. Based on

our quantitative scores from other specimens (described next), we assigned it a velvet score of 1.0.

Data for the remaining 48 species were assessed on spread wings. The whole-wing average velvet score varied from 0 (no velvet in any of the 10 sampled locations) in 11 species (from a variety of bird clades), to 2.0 (velvet of p/b >2) all 10 sample locations, in 7 owl species. Considering the five exposed locations versus five covered locations, among the 30 species with velvet scores >0 but <2 , a strong trend was obvious. All 30 had a larger velvet score in covered locations of the wing than in exposed locations, thus all 30 of these species fall below the 1:1 line in Fig. 2B. That is, among the birds sampled, the velvet was always longer in locations overlain by another feather, and shorter in feather regions exposed to airflow during flapping. Three species, hen harrier (*Circus cyaneus*) and two kite species (*Elanus* spp.) were the most extreme in this respect: each had an average velvet score of zero on exposed parts of the wing, and an average of 2 on covered parts of their wing. This pattern is shown in the images of P10 shown in Fig. 2D–G: a strong gradient of velvet was present right at the point where P9 was in physical contact with P10.

In total, we found velvet was extensive in owls, caprimulgids (except oilbird), was variably expressed in most hawks (and most developed in harriers, *Circus* spp. and kites, *Elanus* spp.) and the American kestrel (*F. sparverius*).

Phylogenetic statistics

There was no support for the echolocation hypothesis (that silencing features such as velvet would evolve in species exhibiting echolocation). Both species with echolocation (oilbird, glossy swiftlet) in our sample each had a velvet score of 0.0, and we did not assess this hypothesis statistically.

The *pgls* models of stealth versus self-masking provided support for both hypotheses (Table 1). Assuming Pagel's $\lambda = 1$, stealth was statistically significant and masking was weakly nonsignificant ($P=0.094$), while allowing Pagel's λ to be an additional parameter in the model yielded an estimate of $\lambda = 0.85$, stealth remained statistically significant and masking was now weakly significant ($P=0.026$). However, in each case, the correlation coefficient between stealth and masking was high (~ 0.4), meaning that multicollinearity prevented the inclusion of an interaction term (stealth \times masking) in the model. Multicollinearity between stealth and masking rendered problematic attempts to

Table 1 Phylogenetic gls statistical tests of stealth and self-masking hypothesis for the evolution of silent flight ($n = 50$ species)

Parameter	Value	P-value	Correlation structure	Log likelihood
Model 1				
Masking	2.94	0.094	Brownian ($\lambda = 1.0$)	-137.7
Stealth	4.17	0.0047		
Intercept	4.64	0.17		
Model 2				
Masking	4.02	0.026	Pagel's $\lambda = 0.85$	-136.5
Stealth	4.23	0.0054		
Intercept	4.40	0.085		

A Stealth \times Masking interaction terms could not be included due to multicollinearity. Stealth and masking were highly correlated (correlation coefficient, Model 1: -0.39 ; Model 2: -0.46).

disentangle these effects statistically when considering all birds together.

Discussion

Does the presence of velvet on the wing feathers of hawks, falcons, nightbirds, and owls evolve to reduce self masking, or to enhance stealth? Our results do not provide a clear answer to this question. This may be because the question itself is ill-posed; self-masking and stealth are not mutually exclusive functions, and could both operate within the same animal in the same predator-prey interaction (Clark et al. 2020). Thus, one perspective on this result is that attempting to set these hypotheses against each other is an example of the pitfalls of the reductionist approach widespread in organismal biology. Although we raise this integrative perspective because we partially agree with it, we hereafter set it aside. The other perspective on this result is that there is evidence, on a clade-by-clade basis, for each of these hypotheses. We may have failed to clearly support one hypothesis at the level of all four clades considered jointly, because one hypothesis is supported in one subclade but the other is supported in another. We address this possibility on a clade-by-clade basis in the second half of the discussion. But first, there are several assumptions that have until now been implicit in our analysis that warrant discussion.

Assumption #1: Does the velvet function to reduce sound? Here we have documented, apparently for the first time, that the velvet is widespread in the wings of a falcon, the American kestrel. Since other relatives had little (Peregrine Falcon) to no (Hobby, Caracara) velvet, this is an independently evolved instance of this trait relative to its origins in nightbirds, hawks, or owls. We have assumed that discovering the presence of the velvet means that the wing

sounds of American kestrel are substantially reduced in some way, relative to those of another similar bird (such as another small falcon); and that the velvet has evolved specifically because it modifies the acoustic signature of American kestrel wing sounds, rather than that it evolved for another reason such that any change in wing sounds is a byproduct of another function. How likely are these two assumptions?

The velvet, in each species that has it, is a modification of the dorsal surface of the distal barbules of feathers, and specifically what had been called “friction barbules” (Lucas and Stettenheim 1972; Wissa et al. 2015). These are modifications of barbules of one feather that are in physical contact with an overlying feather, which acts to prevent slipping between these two adjacent feathers when loaded in shear by aerodynamic forces. Matloff et al. (2020) documented that the inference of friction is incorrect; two feathers loaded in shear resist shearing motions in ways that violate Coulomb’s friction law. Instead, they demonstrated that feathers have features that resist shear by promoting interlocking.

This physical difference in mechanism (interlocking versus friction) does not matter much for the purposes of considering what sounds are produced when two feathers slide against each other. A canonical example of frictional noise is the sound of a piece of sandpaper rubbing against itself, while a canonical example of interlocking noise is the sound of two pieces of velcro being pulled apart (Akay 2002). Both velcro and sandpaper produce similar atonal and broad spectrum sounds. Matloff et al. (2020) documented that barn owls, in addition to the presence of extensive velvet, have lost the lobate cilia that promote interlocking between adjacent feathers. This loss of lobate cilia reduces the resistance to shear of adjacent owl wing and tail feathers (their Fig. 4A), implying that the presence of the velvet trades off with the tendency of the feathers to prevent gaps from appearing in the wing when it is aerodynamically loaded. It remains possible that the velvet has a mechanical function in which it promotes interlocking or friction in other ways, but Matloff et al. (2020)’s data suggest it is unlikely that friction or interlocking is the primary function of the velvet, exclusive of acoustic effects.

Other functions of the velvet, such as for thermoregulation or communication, appear easy to dismiss, since the velvet is best developed (longest, thickest, and densest) is in the wrong physical location (in between the wing and tail feathers: Fig. 2) for either of these functions. There are also suggestions that the velvet is costly: it might make the

feather bearing it harder to preen and harder to apply preen oil to it (Moreno-Rueda 2017), reducing the feather's ability to repel water. There are suggestions that the soft plumage of owls means they suffer rain and getting wet moreso than other birds (Trust 2012), a claim that would be easy to test empirically. The velvet has also been suggested to increase the chances of entanglement with vegetation (Rodríguez et al. 2009). Some species with velvet (barn owl; nightjars) also have a pectinate claw, although this appears to be used to preen specialized head feathers such as rictal bristles (Brauner 1953; Clayton et al. 2010), rather than the velvet. In short, aside from modulating sound production, no other clear functions of the velvet are proposed or known; and multiple plausible drawbacks have been suggested.

Assumption #2: Which species could be selected for stealth? Some of the species for which we have assumed the stealth hypothesis applies (see Fig. 3) may be incorrect. While it seems reasonable to assume that any species preying on rodents (e.g., American kestrel, hawks) could be selected for stealth, it was harder to develop robust assumptions regarding species that prey on insects and other arthropods. We have assumed: *nocturnal aerially insectivorous* birds (great potoo, scissor-tailed nightjar) could be selected for stealth, while diurnal aerial insectivores (e.g., swifts) or nocturnal ground insectivores (elf owl) are not. This assumption is a product of multiple things. Insect hearing has been best studied in the context of predator-prey interactions with bats, but there is growing appreciation that many insects listen for many other types of predators (Yack et al. 2020). Might a small, diurnal insect listen for wing sounds of an approaching swift? This seemed less likely, because swifts tend to eat smaller insects than nightbirds, which often eat fairly large beetles and moths. Swifts tend to approach their prey at higher flight speeds than nightbirds, giving their prey less time to initiate an escape response after hearing the wing sound of an approaching swift. Moreover, stealth is less likely during the day simply because there tends to be more background sound during the day than at night.

We also assumed that both burrowing owl and elf owl, which predominantly eat insects and other arthropods (Henry and Gehlbach 1999; Poulin et al. 2011), are not selected for stealth. This ignores that burrowing owl, under certain circumstances, does feed on vertebrates (Poulin et al. 2011). The reason we assumed stealth was not in play is these two species tend to capture arthropods on the ground, rather than aerially hawking prey from

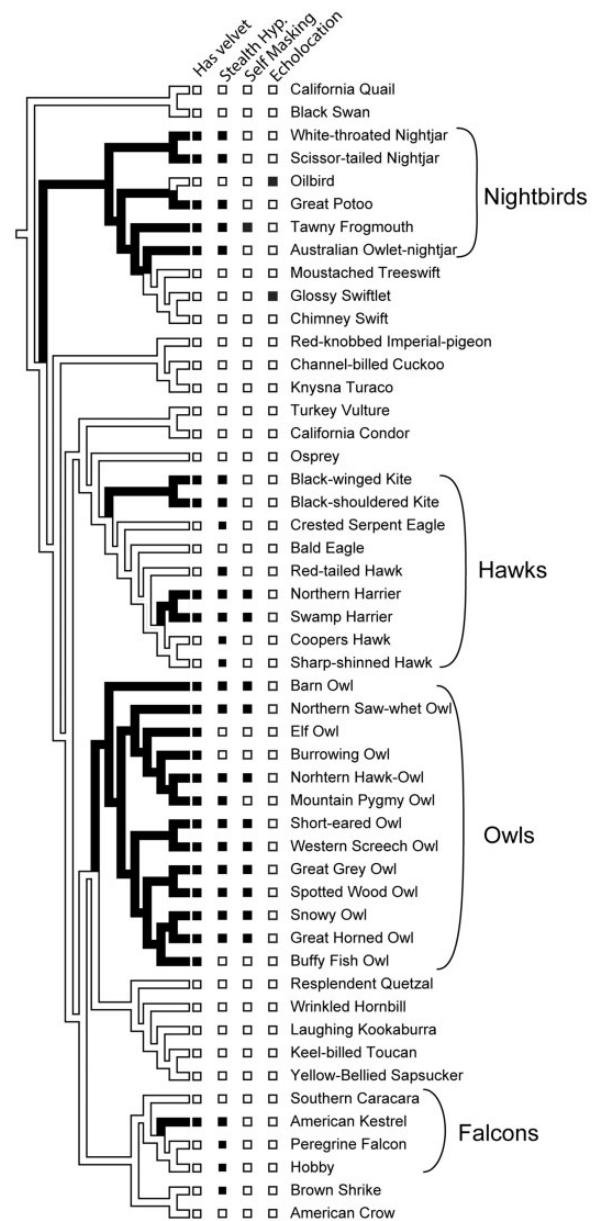


Fig. 3 Phylogenetic reconstruction of species with velvet and three ecological predictors: stealth, self-masking, and echolocation. Velvet presence (black) defined as a velvet score of 0.7–2.0; absence (white) corresponds to velvet score of <0.7.

Note: Phylogenetic reconstruction treating velvet as a binary character is for visualization only; statistics were conducted treating velvet as varying continuously between 0 and 2. Raw data in [Supplementary Table S1](#). There is no support for the hypothesis that the velvet plays a role in self-masking during echolocation, while support for the stealth and self-masking hypotheses is strong and approximately equivalent (see text for more information).

midair. In a review of the evolutionary origins of insect ears, [Strauß and Stumpner \(2015\)](#) suggest insect species that evolve to lose flight also tend to evolve a reduction in hearing ability, and implying

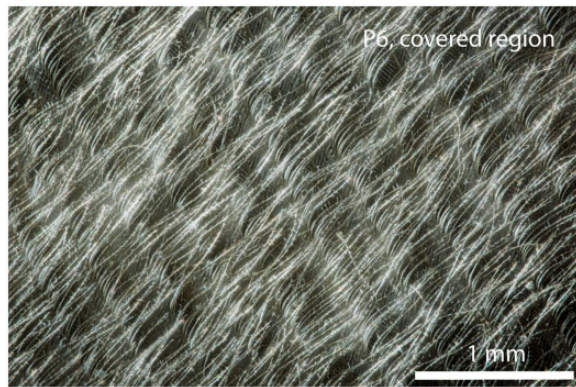


Fig. 4 Velvet on a covered region of P6 of buffy fish-owl (*K. ketupu*). Stacked-focus image, courtesy Anand Varma.

that hearing is less relevant for predator detection for invertebrates on a substrate (Strauß and Stumpner 2015 and references therein). There appear to be few studies showing perched insects listen for predator wing sounds (but, see Jacobs et al. 2008). This is clearly not an especially robust basis for this assumption; absence of evidence of perched arthropods using sound to detect predators is not evidence of absence.

Assumption #3: Which species could be selected to reduce self masking? The issue here is that we have assumed that absence of evidence of hearing use in hunting means bird hearing plays a minor role in hunting. Outside of owls, the role of hearing has been little investigated in raptors. Rice (1982) compared hearing ability of harriers to a few other raptors. Rice (1982) showed that harriers (*Circus* spp.) can locate simulated vole vocalizations (*Microtus* spp.) and would strike a hidden speaker based solely on the vole-sounds it produced, while American kestrels would not. In fact, Rice reports “To ensure that the kestrels could hear the sound stimulus, I gradually increased the volume to very high levels. The kestrels did not even turn to face in the direction of the vole squeak” (Rice 1982, 408). But does this really mean that kestrels are not selected for reduced self-masking, as we have assumed (Fig. 3)? They might be primarily visual hunters, and yet still use sound as a secondary modality, or as a modality during specific parts of the predator–prey interaction. That is, hunting may always be a multimodal interaction, in which case assumption #3 is suspect.

Assumption #4: Quiet flight evolves in predators in a predator–prey interaction. Since it is hawks, owls, falcons, and nightbirds that have velvet, it seems clear that the velvet is a feature predators use to attack prey, rather than the ability of the quiet flyer, in the case of stealth, to avoid being detected by a

conspecific or predator. Self-masking is about hearing prey, rather than hearing a conspecific or a predator. Just because prior research on quiet flight has focused on the predator part of the predator–prey interaction, does not mean these other hypotheses are automatically not worth considering. Small species (especially nightbirds) are prey of owls. Relaxing the assumption that quiet flight evolves in predators does not change the general form of the arguments presented here. Stealth may be about remaining undetected by any other animal’s ears (not just prey), while reducing self-masking may be about listening for any salient sound, not just the sound of prey.

Nightbirds

Nightbirds were once thought to be sister to owls, meaning that quiet flight was assumed to have evolved once in their hypothesized common ancestor. Now that molecular phylogenies have made it unequivocally clear that nightbirds and owls are not close relatives, it also means that quiet flight has clearly evolved convergently more than once within birds (Fig. 3).

Within caprimulgids (Nightbirds), all of the nocturnal species except the fruit-eating oilbird have the velvet (Supplementary Table S1, Fig. 3). There is no evidence nightjars, potoos, or Owlet-nightjars use sound to hunt. These three nightbird subclades primarily catch insects on the wing, either by coursing (nighthawks, which are within nightjars), or by perching on a substrate, then flying up to catch insects spotted flying overhead (Potoo, many nightjars, and owlet-nightjars). Species accounts tacitly assume that prey acquisition is visual (Woods et al. 2005), presumably as flying insects make very little sound. The presence of the velvet therefore supports the stealth hypothesis in these species, since an essential component necessary for the self-masking hypothesis (prey make sounds audible to the predator) is absent, but airborne insects should be sensitive to bird wing sounds, including ultrasound made by feathers rubbing against feathers (Fournier et al. 2013; Clark et al. 2020; Yack et al. 2020).

Within nightbirds, frogmouths in the genus *Podargus* have a subtle, important difference in foraging ecology. Like most other nightbirds, frogmouths sit on a perch, scanning for potential prey, but instead of flying up to intercept prey flying above, one hunting strategy they employ is similar to owl hunting: they detect prey on the ground below them, then fly down to catch it (Kaplan 2018). Terrestrial insect prey may make rustling or footstep

sounds that permit them to be heard by predators (Goerlitz et al. 2008) at greater distances than the wing sounds of flying insects. Therefore, there is greater scope for quiet flight to evolve under the self-masking hypothesis in frogmouths. Moreover, while frogmouths mainly eat insects, they do sometimes eat vertebrates such as mice (Kaplan 2018). The observation of a frogmouth catching a mouse on a moonless night in dense thistles (Davey and Einoder 2001) suggested the mouse was heard by the frogmouth, rather than seen. Apart from this incidental observation, whether frogmouths use hearing to detect prey remains virtually unstudied (Swanson and Sanderson 1999). Frogmouths have the highest velvet score of any nightbird we measured (Fig. 2B) and also have a leading-edge comb (Mascha 1905), unlike the other nightbirds. That is, their silencing features are better developed than other nightbirds. This apparent correlation between an increase in silencing features and an increased use of sound to hunt prey would strongly support the self-masking hypothesis. We say “would” because many of the statements in this paragraph are conjectural: the role of sound in frogmouth hunting deserves further research attention.

Hawks

We found the presence of a little bit of velvet was widespread in hawks, including in fish-eating species with little apparent need for either stealth or self-masking: bald eagle and osprey had an average velvet score of 0.6 and 0.5, respectively (Supplementary Table S1). Species not known to use sound themselves, but which prey on mammals (e.g., Red-tailed Hawk, score: 0.7) had more, while the two hawk clades suggested or known to locate prey acoustically (kites and harriers respectively) had the greatest velvet scores (Supplementary Table S1; Rice 1982; Negro et al. 2006). This again seems to support both hypotheses: stealth selects for some silencing features (hawks generally), and self-masking selects for more (kites and harriers), although the presence of a little bit of velvet in fish-eating hawks (osprey and bald eagle) supports neither hypothesis.

Falcons

Here we document that American kestrels also have the velvet, while other relatives have less (Peregrine Falcon) or none (Supplementary Table S1). Modern bird phylogenies have made clear that falcons and hawks are not close relatives (Fig. 3), implying that this plumage similarity has evolved convergently. Within falcons, American kestrels have also

convergently evolved a relatively hawk-like foraging strategy: they fly slowly when hunting (unlike some other falcons such as Peregrine Falcon) and are often seen “kiting,” rapidly flapping their wings in a wind-assisted hover above prey. This behavior is named for the hunting strategy of kites (*Elanus* spp.) (Smallwood and Bird 2002). Here we have documented that they have the same velvet as kites (Fig. 2F and G). Perhaps rapidly flapping the wings during this particular mode of foraging produces more sound (i.e., perhaps the wing-feathers may rub a lot when the wings are flapped rapidly).

Owls

Our most surprising result within owls is the finding that buffy fish-owl (*Ketupa ketupu*) had extensive velvet throughout its wing, and a velvet score of 1.5 (Fig. 4), as much velvet as owls such as northern hawk-owl, mountain pygmy owl, or elf owl (velvet scores: 1.5, 1.4, and 1.3, respectively; Supplementary Table S1). This contradicts a widely repeated claim. Graham (1934) asserted that fishing owls had lost the velvet, but gave no indication of how he assessed this. Graham’s claim of the absence of velvet in fish-owls has been re-repeated many times since (e.g., Lilley 1998; Bachmann and Wagner 2016), apparently without independent verification until now. The feathers of the wing specimen we examined (BM #117151) felt stiffer to the touch than feathers of other owls; they felt like hawk feathers, not owl feathers. We attribute this qualitative difference not to the velvet, but to a change in the flexural stiffness of the entire vane. Perhaps Graham mistook this increased rigidity to be caused by an absence of the velvet. Graham’s “3-traits” paradigm in which he suggests quiet flight is achieved by exactly three wing features (the comb, fringe, and velvet) is an oversimplification (Clark et al. 2020). The softness of owl feathers is not caused by the velvet alone. And the role of flexural stiffness of feather vanes in sound production is unclear.

The other result that surprised us was the amount of velvet present in mountain pygmy-owl (*Glaucidium gnoma*). The Birds of North America (BNA) species account for northern pygmy-owl (*G. californicum*) states that “Wings make whistle-like noise when Pygmy-owl flies” (Holt and Petersen 2000). One source of “whistle-like” (i.e., tonal) sound is aeroelastic flutter (Clark and Prum 2015); another might be frictional interactions, as in the “swish” sound made by displaying Greater Sagegrouse as they rub their wings against stiffened breast-feathers (Koch et al. 2015). Either of these

mechanisms should be easy for pygmy owls to suppress. Why an animal with noisy flight would also have extensive velvet is unclear. Recordings of the wing sounds of a pygmy owl would reveal whether this species does have louder flight than other species of bird.

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Supplementary data

Supplementary data available at *ICB* online.

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