Correlated evolution of white spots on ears and closed habitat preferences in felids

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Abstract

The pigmentation patterns of many carnivorous mammals comprise contrasting white patches of hair in different parts of the body whose evolution remains largely misunderstood. Some felids (Felidae) exhibit conspicuous white spots on the posterior part of the ears, while the ear color of others is uniform. On the basis that ear movement in felids has a role in intraspecific communication and that color contrast enhances detection, here it is hypothesized that white spots on ears may be particularly adaptive under conditions of poor visibility and thus be associated with the occupancy of closed habitats. This prediction was tested using phylogenetic logistic regression models with all species of extant felids. Results show a clear association between the occurrence of white spots on ears and preference for closed habitats, and this is independent of body size and whether species that occupy both closed and open habitats are considered as closed- or open-habitat specialists. Phylogenetic signal analyses indicate that the occurrence of white spots on ears is a highly conserved trait while habitat preferences are evolutionarily labile, suggesting that the presence of white spots may have partly contributed to the adaptation of felids to closed habitats. These findings indicate that some subtle pigment traits have fulfilled a significant role in determining the success of habitat occupancy by felids and possibly other mammals, which in turn has driven the evolutionary maintenance of such traits.

Keywords amplifiers · black-and-white patterns · ear movement · Felidae · habitat adaptation · mammalian color patterns

50 **Introduction**

51 Some animals exhibit white patches that contrast with dark colors in the body. The
52 combination of black and white creates very conspicuous traits that are highly efficient at
53 enhancing detection by others, given the high contrast that they form (Osorio et al. 1999;
54 Schmidt et al. 2004). Contrasting white marks confer different kind of information, which
55 has favored their evolution. For example, contrasting white marks in birds have evolved as
56 signals of presence in species that benefit from social foraging (Beauchamp and Heeb
57 2001) or as amplifiers of movement in species that perform ritualized displays (Galván
58 2008). In mammals, the function of contrasting coloration has been intensively discussed,
59 yet no concluding evidence for the exact information conferred by these color patches has
60 been obtained as the investigation of possible functions (Caro 2011; Caro et al. 2017) has
61 not considered predictions from signal theory (Hasson 1997). The reasons that have led to
62 the evolution of contrasting white marks in mammals therefore remain unclear.

63 However, the factors driving the evolution of white marks in mammals are expected
64 to be similar to those in birds. Thus, habitat is known to exert an effect on the evolution of
65 contrasting white marks in at least some species of birds that commonly fall prey to other
66 birds or mammals, as these marks facilitate anti-predator signaling in gregarious species
67 that inhabit open habitats (Stang and McRae 2009). While it is unknown whether habitat
68 has a similar effect on the evolution of white marks in predatory birds, it is likely that
69 habitat also has an effect on the presence of white marks in mammals. Felids (family
70 Felidae) constitute appropriate models to investigate this hypothesis, as some species
71 exhibit conspicuous black-and-white spots on the posterior part of the ears (Fig. 1). It is
72 clear that felids use the movement of their ears in intraspecific communication (Kingdon
73 1977; Kitchener et al. 2010; Stanton et al. 2015). Therefore, contrasting white spots may
74 improve the perception of the information transferred with ear movements and thus
75 function as amplifiers of such information like contrasting white marks in birds that perform

movement displays (Galván 2018). As contrasting white marks improve detection (see above), the white spots of felids' ears should be particularly efficient under poor light conditions such as those prevailing in closed habitats.

A correlated evolution of white spots on ears and habitat occupancy in felids is predicted, as white spots should be expected to have evolved more frequently in species that inhabit closed habitats than in those that inhabit open habitats. This prediction was tested on the entire Felidae, with the aim of contributing to the knowledge of factors driving the evolution of appearance in mammals. As the spatial distance for detecting conspecifics (i.e., viewing distance) is positively related to body size in both mammals and birds (Kiltie 2000), the analyses were conducted by controlling for the effect of the body size of species, for which body mass constitutes a surrogate.

Methods

White spots on ears and body mass

The presence or absence of contrasting white spots on the posterior part of ears were determined by examining the illustrations of felids in Wilson and Mittermeier (2009) and photographs in www.iucnredlist.org. The body mass of felid species was obtained from Wilson and Mittermeier (2009). As the body mass of females was not available in all species, the maximum value provided for males was assigned to the species.

Habitat type preferences

The habitat preferences of felid species were investigated by determining if they occupy closed or open habitats following previous classifications made by Ortolani (1999) and Werdelin et al. (2010). Thus, closed habitats comprised forests, rain forests, riparian or brush and scrub habitats, while open habitats comprised grasslands, deserts, and arctic habitats (Ortolani 1999). The same assignment of habitat non-specialists made by Werdelin

et al. (2010) to some species that occupy both closed and open habitats was followed, and separate analyses considering assigning closed or open habitats to these species were conducted (see below).

Phylogenetic analyses

Whether the presence of white spots on ears is associated to closed habitats in 37 species of felids (Fig. 2) was tested by conducting a phylogenetic logistic regression model (Ives and Garland 2010) with presence/absence of white spots as a response variable, habitat preference (closed vs. open) as a fixed factor, and body mass (in $\log_{10}$) as a covariate. The simulation algorithm implemented by Ho and Ané (2014) in the R package *phylolm* was employed, using 1000 permutations. Relationships between felid species were established from the phylogeny of Felidae provided by Johnson et al. (2006). The Sunda clouded leopard *Neofelis diardi* and the Chinese mountain cat *Felis bieti* were included as two additional species, as these are considered separate species that are sister to the clouded leopard *Neofelis nebulosa* and the European wildcat *Felis silvestris*, respectively, by Wilson and Mittermeier (2009) (Fig. 2).

Lastly, the phylogenetic signal in the occurrence of white spots on ears and in habitat preferences were estimated using the parameter D developed by Fritz and Purvis (2010) for binary traits. The estimated value of D and associated p -values for $H_0: D = 1$ was calculated with the R package *caper* (Orme et al. 2013). When $D = 1$, a random phylogenetic structure (i.e., absence of phylogenetic signal) exists, whereas a D value of 0 is indicative of a Brownian motion mode of evolution (i.e., changes in the trait along the phylogeny are proportional to the degree of relatedness among species). Negative D values are indicative of highly clustered traits (Fritz and Purvis 2010). Separate phylogenetic logistic regression models and D analyses assigning closed or open habitats to the species that occupy both closed and open habitats were conducted.

Data availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Out of 37 species of felids, 25 (68%) exhibit contrasting white spots on the posterior part of the ears, while 12 (32%) do not have white spots (Fig. 2). The estimated D value for the occurrence of white spots was -6.91, which was significantly different from a random phylogenetic structure ($p = 0.003$). In contrast, the estimated D value for habitat preferences when closed habitats were assigned to species that occupy both closed and open habitats (-0.88) was not significantly different from 1 ($p = 0.227$), indicating absence of phylogenetic signal. When open habitats were assigned to these species, however, the estimated D value (-6.97) indicated significant phylogenetic signal ($p = 0.004$).

The results of phylogenetic logistic regression models indicated that the effect of body mass was not significant at explaining interspecific variability in the occurrence of white spots on ears, either assigning closed habitats to species that occupy both closed and open habitats (estimate = 0.06, $z = 0.08$, $p = 0.933$) or assigning open habitats to those species (estimate = 0.67, $z = 0.98$, $p = 0.328$). Therefore body mass was removed from the models. The effect of habitat preferences in the final models was significant, again independently of whether closed habitats were assigned to species that occupy both closed and open habitats (estimate = 2.56, $z = 3.06$, $p = 0.002$) or open habitats were assigned to these species (estimate = 2.11, $z = 2.15$, $p = 0.032$). This effect of habitat preferences was due to an association of the presence of white spots on ears to closed habitats (Fig. 3).

Discussion

As predicted on the basis that felids make an use of ear movement to communicate with conspecifics (Kingdon 1977; Kitchener et al. 2010; Stanton et al. 2015), and that contrasting colors improve detection (Osorio et al. 1999; Schmidt et al. 2004), a correlated evolution of white spots on ears and occupancy of closed habitats in the Felidae family was found. High vegetation density limits visibility in closed habitats, leading to a higher prevalence of acoustic communication traits in mammals inhabiting closed habitats and a higher prevalence of visual traits in those inhabiting open habitats (Ey and Fischer 2009). However, evolutionary solutions to habitat limitations frequently arise, mediated by visual traits that increase the perception of other signals or cues (i.e., amplifiers; Galván 2008; Galván and Sanz 2009) or that simply facilitate the detection of the bearer by others (i.e., signals of presence; Beauchamp and Heeb 2001). As ear movement might confer any kind of information to conspecifics in felids and thus constitute a signal itself (see above), it is likely that the white spots of ears actually act as amplifiers of ear movement, similar to white plumage patches that act as amplifiers of body movement during ritualized displays in birds (Galván 2008). The concept of amplifier has never been applied to understand color pattern evolution in mammals, but this may explain at least the higher frequency of felids with white spots on ears in closed habitats. If white spots actually facilitate the visual communication of felids in closed habitats, it should be expected that the adaptive value of acoustic signals is reduced as compared to felids in closed habitats without white spots. This should lead to predict a reduction in the use of acoustic communication, or a higher prevalence of close-range in contrast to long-range vocalizations (Peters and Tonkin-Leyhausen 1999), in felids presenting white spots and inhabiting closed habitats. This should be considered by future studies.

The estimates of phylogenetic signal in the studied traits provide some indication of how white spot occurrence and habitat preferences may have influenced each other

during the evolution of Felidae. There is strong phylogenetic signal in the occurrence of white spots on ears, and the large negative D value (-6.91) actually indicates that this is a highly clustered trait in the felid phylogeny (Fritz and Purvis 2010). This means that the occurrence of white spots on ears is a highly conservative trait. The loss of phylogenetic signal in a trait occurs when some species in a phylogeny obtain adaptation to certain environmental conditions (Blomberg et al. 2003). Thus, it is not likely that the evolution of white spots on ears in felids has been driven by adaptive benefits under certain environmental conditions, as the evolution of this trait follows phylogenetic inertia in a strict manner. Consequently, white spots on ears do not seem to be of relevance for the adaptation of felids. In contrast, habitat preferences show an opposite pattern, because they show random phylogenetic structure, at least when closed habitats are assigned as a preferred habitat type for species that occupy both closed and open habitats. This is indicative of a loss of phylogenetic signal in the habitat preferences of felids, suggesting that some species obtained adaptation after occupying some habitats. Habitat preferences are therefore labile, while white spots on ears are evolutionarily fixed. Habitat preferences cannot thus have influenced the evolution of white spots on ears, but white spots may have contributed, at least partly, to the adaptation of felids to closed habitats. A similar contribution to the successful occupancy of closed habitats by felids may have been provided by the presence of slit-like pupils in some species (Mattern and McLennan 2000; Werdelin et al. 2010).

Pigmentation patterns in mammals are extraordinarily diverse, and carnivorans probably represent the group with a highest heterogeneous diversity of patterns (Ortolani 1999). However, the reasons of the origin and maintenance of such diversity are largely unknown, probably because of a lack of functional hypotheses to test. The present study contributes to this question in felids, where white spots on ears may have contributed to the adaptation to closed habitats. This, in turn, may have led to the maintenance of white

spots on ears during the evolution of felids. The diverse optical properties of pigment traits actually constitute important factors that enhance or constrain the occupancy of some habitats by animals (Galván et al. 2018), an association that should thus be considered as a potential general explanation for a significant proportion of mammalian phenotypes.

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281 **Legends to figures:**

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283 **Fig. 1** Examples of felids with white spots on the posterior part of the ears (A, Iberian lynx
284 *Lynx pardinus*) and without white spots (B, European wildcat *Felis silvestris*). Credits of
285 photographs: Rafael Palomo Santana.

286

287 **Fig. 2** Phylogenetic tree of Felidae used in the study. Symbols indicate presence/absence
288 of white spots on the posterior part of the ears and habitat preferences of the species.

289

290 **Fig. 3** Number of felid species with (striped bars) and without (black bars) white spots on
291 the posterior part of the ears in relation to habitat preferences. Species that occur in both
292 closed and open habitats are separately considered as closed-habitat specialists (A) and
293 open-habitat specialists (B).