

Aggression and fitness differences between plumage morphs in the common buzzard (*Buteo buteo*)

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Genetic plumage polymorphism in birds is increasingly recognized as a potentially important trait influencing birds' life histories. In the common buzzard *Buteo buteo*, the 3 color morphs vary in lifetime reproductive success (LRS), but the proximate mechanisms leading to these differences are unknown. We first confirmed the stability of the fitness differences found previously, using a greatly extended LRS data set. To find potential causes for these differences, we experimentally studied variation in aggressive behavior of the morphs, both against an interspecific predator and intraspecific competitors. The morphs showed substantial variation in aggressive behavior. Light-colored males were most aggressive toward an interspecific predator, followed by intermediate and dark males. In females, this pattern was reversed, resulting in sex-related differences of aggression in 2 morphs. When defending their territory against intraspecific competitors, no absolute difference in aggression was found, but the morphs reacted strongest toward intruders of a morph similar to their own. This suggests that aggression differs both between and within morphs, leading to a complex pattern on the population level. Coupled with the strong fitness differences, our results suggest that the genetic basis of the polymorphism has far-reaching behavioral consequences. **Key words:** aggression, fitness, polymorphism, predation risk, territory defense. [*Behav Ecol* 20:180–185 (2009)]

Polymorphism in plumage color of birds is a phenomenon that is widespread but little understood (Galeotti et al. 2003; Roulin 2004). True, non-condition-dependent genetic polymorphism within the same age and sex occurs in 334 bird species of 53 families (Galeotti et al. 2003) and ranges from small differences such as the color of eye stripes to entirely different plumages. Many hypotheses for the evolution and maintenance of polymorphisms are based on disruptive selection, predicting fitness advantages for extreme phenotypes or morphs (Clarke 1962; Van Valen 1965; Arnason 1978; Galeotti and Cesaris 1996; Greene et al. 2000; Fowlie and Krüger 2003).

Far more puzzling, however, are species such as the common buzzard *Buteo buteo*, in which several morphs occur but no fitness advantage for the extreme morphs has been found. The common buzzard has 3 distinct color morphs (dark, intermediate, and light), with individuals having predominantly white, brown, or mixed plumage on the underside of their torso and wings (Glutz et al. 1971; Melde 2004). Fitness differences between these morphs are substantial in our population, with intermediate birds achieving both longer breeding life span and higher reproductive success per season (Krüger and Lindström 2001; Krüger et al. 2001). This has been ascribed to heterozygote advantage because there is strong evidence that the intermediate morph is heterozygous (Krüger et al. 2001). However, the proximate causes of the fitness advantage are not known. Inbreeding avoidance has often been assumed to be a cause for heterosis (Brown 1997), but the assortative mating system found in the common buzzard suggests that there is no strong selection pressure on finding genetically dissimilar mates. Rather, the fitness advantage of intermediates seems to be more directly

linked to their plumage polymorphism. There are 3 nonmutually exclusive potential mechanisms for this: 1) the alleles for plumage color could be tightly linked to other fitness-influencing traits; 2) plumage color could have direct fitness effects, such as improved crypsis or thermoregulation; 3) parts of the physiological mechanisms creating plumage morph could affect other traits which then, in turn, affect fitness (pleiotropic effects).

In this paper, we concentrate on a fitness-related trait, which could be linked to the plumage polymorphism through either genetic linkage or pleiotropy: aggressive behavior. We test whether the plumage morphs of the common buzzard differ in their defense against predators and competitors in a way that could generate the observed differences in fitness. Whereas behavior toward predators could influence survival and reproduction, territory defense against intraspecific competitors is likely to affect reproductive success only. Access to suitable breeding territories is a limiting factor in our study area, with mature individuals floating or queuing in the population each year (Krüger and Lindström 2001). Additionally, territories vary in quality. Together with plumage morph, territory characteristics are important predictors for an individual's lifetime reproductive success (LRS) (Krüger 2002b). Important factors include size and shape of the forest and different measures of human disturbances (also see Krüger 2002a). Intermediate pairs breed furthest from human disturbances (Boerner 2005) and occupy a disproportionate number of "popular" territories (Krüger 2002b). In this study, the number of years a territory was occupied served as a measure for its quality, arguing that after the death of the previous owners, better territories would be occupied again sooner than poor territories. As the study lasted several times the length of the common buzzard's average breeding life span, the differences in longevity between the morphs did not confound this result. Overall, these results suggest that intermediate pairs obtain better territories than either dark or light pairs. Therefore, we expected the intermediate morph to be most aggressive,

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achieving its high LRS through defense against potential predators and through aggression toward conspecifics in competition for breeding territories.

We designed 2 experiments in order to independently test for aggressive behavior toward potential predators and conspecific competitors. In the first experiment, we presented a stuffed dummy of the Eurasian eagle owl *Bubo bubo* close to the nest of a buzzard breeding pair and compared the response of the different morphs. To test the reaction toward competitors, we used a 2-way factorial design: we presented 1 of 3 stuffed buzzard dummies (one of each morph) near the nests of breeding pairs of each morph.

The population where our experiments and the long-term fitness study were carried out has grown over the past 18 years. This increase is most likely due to more favorable abiotic conditions with much milder winters, which are known to affect buzzard populations significantly (Glutz et al. 1971). This could have affected estimates of average reproductive success of the morphs. Therefore, we include a brief analysis of LRS data, including 6 more years of data after the publication of the first results (Krüger et al. 2001) to confirm that the fitness differences are not a short-term transitional phenomenon.

MATERIALS AND METHODS

Study site and population

The study was conducted over 18 years between 1989 and 2006 in eastern Westphalia, Germany (8°25' E and 52°6' N), with data on LRS collected continuously throughout the entire study period and experimental data collected from 2001 to 2006. The study population is scattered over small to medium-sized patches of deciduous, coniferous, and mixed forest, surrounded by cultivated land and spread out over 300 km² (for a more detailed description, see Krüger and Lindström 2001). During the study period, buzzard density varied between 12.7 and 42.7 pairs per 100 km².

Data on individual fitness were collected each year by searching for nests in early spring and visiting each occupied nest at least 3 times during the breeding season, determining the number of fledglings by observation from the ground. Since 2002, all nests were climbed to determine reproductive success. All experiments were conducted at active nests during the breeding season. Interspecific aggression was tested in 2001–2004 and intraspecific aggression in 2005 and 2006.

Fitness data

Buzzards were drawn or photographed, and the high variation in plumage color and especially pigmentation pattern (Glutz et al. 1971; Cramp and Simmons 1980) allowed individuals to be recognized individually from year to year without marking (see Glaubrecht 1983; Janes 1984; for similar approaches, Bateson 1977; for reliability tests on other species, Scott 1979). Since 2002, all chicks and some adults have been color ringed, so that around 15% of the adult population is easily identifiable through these rings. As for other resident bird species, it is assumed that once an adult individual is not found in the population for 2 years or more, it has died (Newton 1989). Rarely, birds skipped a breeding attempt, which is why 2 years were taken as the threshold to assume death.

We were able to determine the LRS of 274 males and 239 females. LRS is a major component of individual fitness regardless of the definition adopted (Brommer et al. 1998), and recent evidence suggests that it is at least as informative as rate-sensitive measures such as the individual fitness λ (Brommer et al. 2002).

Behavioral response toward a predator

To measure aggression against a potential nest predator, a stuffed adult female Eurasian eagle owl (*Bubo bubo*) was mounted on a tripod and presented to breeding pairs during the chick-rearing period. Eurasian eagle owls kill buzzards as prey (Serrano 2000), and buzzards and other raptors respond with alarm calls and/or mock attacks to the presence of eagle owls (Bub 1991; Zuberogitia et al. 2008). We used 2 different dummies, which did not differ in the response they evoked. The dummy eagle owl was positioned within 50 m of the buzzard nest, placing it where it was highly visible and accessible at the edge of the forest. Males and females of all 3 buzzard morphs were tested ($N = 4$ dark females, 7 dark males, 30 intermediate females, 31 intermediate males, 20 light females, and 16 light males).

The buzzards' behavior was observed for 1 h after their first reaction to the eagle owl. Aggression was scored separately for males and females on a scale from 0 to 2 (0: calls and circling above the dummy; 1: mock attacks on the dummy without making physical contact with it; and 2: attacks with physical contact).

To explain the variance in the aggression score, we used a general linear mixed model (GLMM) for each sex, using morph as the primary explanatory variable and controlling for year (random factor), chick age, and number of chicks in the nest (covariates). Variables that did not explain a significant proportion of variation in the data ($P > 0.1$) were removed from the final model.

Behavioral response toward a competitor

Aggression toward intraspecific competitors was measured by mounting a stuffed male buzzard on a tripod standing on the ground within 50 m of the nest. In raptors, territory intrusion and defense are predominantly done by males (Wiklund and Stigh 1983; Andersson and Wiklund 1987). Therefore, using a male dummy was less likely to confound our results due to being perceived as a potential mating partner by the relevant sex. We mainly tested breeding pairs in which both partners were clearly assignable to the same morph (32 intermediate and 11 light pairs). However, due to the rarity of the extreme morphs, we had to include pairs in which one partner belonged to the intermediate morph but had a tendency toward its partner's extreme morph (17 dark pairs and 8 light pairs). These individuals belonged to the darkest or lightest third of the intermediate group, respectively. The usage of these pairs should, if anything, result in more conservative estimates of aggression differences between the morphs. Due to their rarity, some of the dark pairs had to be tested in both years, using different dummies. To control for this, we entered pair ID as a random factor into our model. As this factor was not significant, it was later dropped from the model.

We used 2 buzzard dummies, one of them intermediate and the other one light. In 2006, the latter was dyed to resemble the dark morph. We tested museum specimens of each morph for UV reflectance in their plumage to rule out potential effects of covering UV markings by dyeing the dummy. No such markings were found in adult buzzards. Each of the dummies was presented 3 times to the same breeding pairs, and each dummy was presented to pairs of all 3 morphs. During the first 20 min of the experiment, buzzard alarm calls were played from loudspeakers beneath the dummy to attract attention and mark the dummy as a hostile intruder.

Behavior was measured using 5 different variables over 50 min for each trial: average distance from the dummy, smallest distance to the dummy, number of calls given, average length of the first 10 call intervals, and time until the first reaction

after the playback of alarm calls had stopped. Behavior recording began immediately after positioning the dummy and starting the call playback. Obtaining fine-scaled data on the pairs' position in relation to the dummy required the observer to remain in proximity of the dummy but hidden from the pairs' attention. This made it impossible to follow the movement of each partner individually and to identify them correctly at all times. Therefore, we present a combined pair score, including all reactions recorded, irrespective of sex. As most territory defense is done by the males (Wiklund and Stigh 1983; Andersson and Wiklund 1987), these scores mainly represent the male pattern of response. However, as the influence of the female cannot be quantified, we refer to the aggression as the response given jointly by the pair.

We tested the influence of year and dummy position (random factors), Julian date, chick age, number of chicks (covariates) in analyses of variance (ANOVAs) of repeated measurements for all variables. Because no significant effects could be found, data from all 3 trials at each nest were pooled for the subsequent analyses. The factor year showed no significant effect and was dropped from the model as well. On 4 occasions, pairs neither called nor approached the dummy. As the number of calls was zero, the interval length between calls was set to 30 min (length of observation). Average and minimum distance to the dummy were set to 250 m, the maximum distance observed in other pairs. All behavioral variables were then entered into a principal components analysis to accommodate the great difference in variances of the variables. Only components with an Eigenvalue above one were considered. The principal component score was tested in a general linear model with both dummy morph and breeding pair morph as fixed factors and pair ID as a random factor. We report only the minimum adequate model.

RESULTS

Fitness differences between the plumage morphs

There were highly significant differences in LRS between the 3 plumage morphs in both male and female common buzzards (Figure 1; $F_{2,271} = 10.865$, $P < 0.001$ and $F_{2,236} = 26.375$, $P < 0.001$, respectively). Post hoc tests showed that these overall differences resulted from dark and light morphs having significantly lower fitness than the intermediate morph in males (dark vs. intermediate: $P = 0.002$, light vs. intermediate: $P = 0.001$) and females (dark vs. intermediate: $P = 0.001$, light vs. intermediate: $P = 0.001$). Differences between the 2 extreme morphs were not significant in either males ($P = 0.975$) or females ($P = 0.762$). These differences between the morphs were not only due to differences in mean life span as a breeder in males ($F_{2,271} = 5.635$, $P = 0.004$) and females ($F_{2,236} = 16.937$, $P < 0.001$), but residual LRS (controlling for life span) also differed between the plumage morphs in males ($F_{2,271} = 5.140$, $P = 0.006$) and females ($F_{2,236} = 7.414$, $P = 0.001$).

There were no significant differences between the sexes in either overall LRS ($F_{1,511} = 0.191$, $P = 0.662$) or life span as a breeder ($F_{1,511} = 2.227$, $P = 0.136$).

Behavioral response to a predator

Males of the different plumage morphs differed significantly in their aggressive response level to the eagle owl dummy (Figure 2; $F_{2,51} = 7.709$, $P = 0.001$). Light males were significantly more aggressive than both dark ($P = 0.007$) and intermediate males ($P = 0.003$), whereas the difference between dark and intermediate males was not significant ($P = 0.659$). There was no significant effect of the number of chicks in the nest ($F_{2,51} = 1.687$, $P = 0.195$) or their age ($r_{52} = -0.009$, $P = 0.950$).

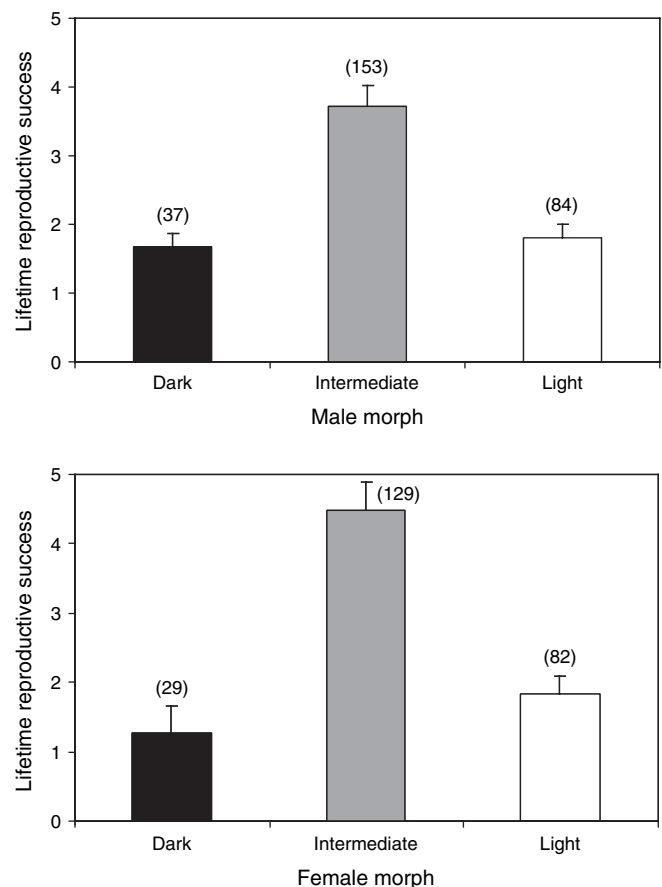


Figure 1

Mean LRS (+standard error) of the different plumage morphs for male and female common buzzards. Data are shown untransformed with statistical analyses being done on log-transformed data. Numbers above error bars are the sample sizes.

There were also significant differences in aggression between females of different plumage morphs (Figure 2; $F_{2,51} = 3.306$, $P = 0.045$), but in the opposite direction. Dark females were significantly more aggressive than both light ($P = 0.045$) and intermediate females ($P = 0.041$), whereas the difference between light and intermediate females was not significant ($P = 0.997$). There was again no significant effect of the number of chicks in the nest ($F_{2,51} = 0.769$, $P = 0.469$) or their age ($r_{52} = -0.031$, $P = 0.826$).

There was also a significant difference between the sexes in their aggressive response level, with males being more aggressive than females ($t_{53} = 2.245$, $P = 0.029$).

Behavioral response to a competitor

The principal component analysis resulted in one component explaining 77.2% of the total variance (Eigenvalue: 3.859). Four of the factors loaded positively onto the component, one negatively (canonical correlations: average distance from dummy: 0.910; smallest distance from dummy: 0.836; average call interval: 0.945; time until first reaction: 0.943; number of calls: -0.740). Because this resulted in increasing aggression being indicated by decreasing values, we multiplied the component's score values by -1 to obtain a more intuitive illustration of aggression. The aggression score differed significantly between the 9 experimental groups (Figure 3; $F_{8,58} = 2.505$, $P = 0.021$). This was due to a significant interaction between

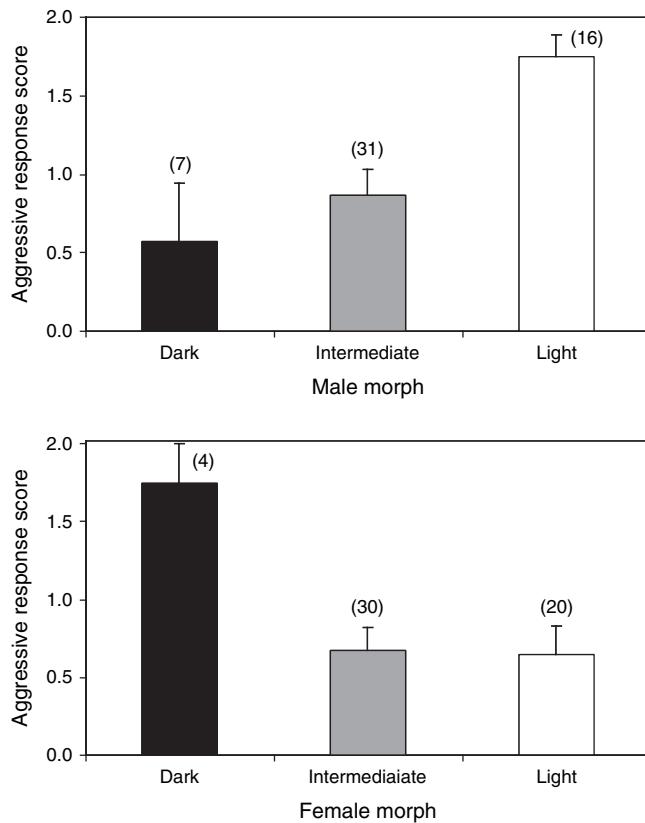


Figure 2
Mean aggressive response scores (+standard error) in the eagle owl experiment of the different plumage morphs for male and female common buzzards. Numbers above error bars are the sample sizes.

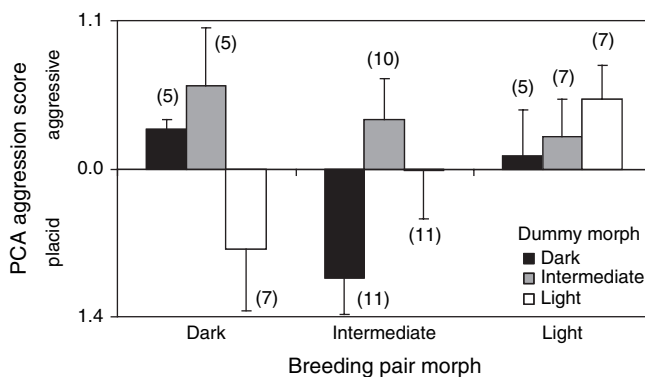


Figure 3
Principal components analysis aggression scores (+standard error) in the buzzard competitor experiment of the different plumage morphs and the different dummy morphs. Numbers above error bars are the sample sizes.

the treatment (dummy morph) and the morph of the breeding pair ($F_{4,62} = 2.675$, $P = 0.041$). Buzzards reacted more aggressively to a dummy of their own morph, with the exception of dark pairs who showed more aggression toward the intermediate than the dark dummy (see Figure 3). None of the morphs showed an overall stronger reaction if dummy morph was not taken into account ($F_{2,64} = 2.261$, $P = 0.113$), and no dummy morph elicited consistently higher aggression than the other dummies if pair morph was ignored ($F_{2,64} = 1.306$,

$P = 0.279$). A further ANOVA including only those dummy morph/breeding pair morph combinations that appeared to result in highest aggression (see Figure 3) suggests that there are no differences in maximum aggression shown by any of the morphs either ($F_{2,21} = 0.219$, $P = 0.805$). There was no significant effect of the number of chicks in the nest or their age (ANOVA of repeated measurements: all P values > 0.2).

DISCUSSION

Plumage polymorphism is associated with aggression differences (Tuttle 2003) and fitness differences between morphs in several bird species, notably predatory birds (Galeotti et al. 2003; Roulin 2004; Brommer et al. 2005). In our study, we tested whether behavioral differences can explain the fitness of the morphs in the common buzzard. The results show that buzzard morphs follow different but apparently simple behavioral patterns when confronted with an interspecific predator, whereas their reaction toward an intraspecific competitor appears to be the result of a general but more complex pattern.

Buzzards' aggression toward a predator seems to depend primarily on their own morphs and, in case of females, on the behavior (and therefore, morph) of their partner. In the light and intermediate morphs, nest sites were defended more vigorously by males than by females. This is the expected pattern, as female buzzards rarely leave the nest during the chick-rearing period (Cramp and Simmons 1980). Interestingly, the unexpectedly high aggression of dark females occurred only after their partner had left the territory in response to the presence of the eagle owl dummy, suggesting that dark females may have been forced to compensate for their partners lack of defense.

As eagle owls are a major predator of raptor chicks and adults (Serrano 2000), a buzzard's behavior toward them is directly fitness relevant (Krüger 2008). Thus, dark males' avoidance of contact with predators may be adaptive outside the breeding season, but it carries potentially high costs during the nestling stage of the brood. If the males' departure from the territory triggers the females to leave the nest, chicks are potentially exposed to adverse weather conditions and are more vulnerable to predators. This trade-off between adult survival and reproductive success seems to be inverted in the light morph, leading to more confrontations between light individuals and predators. Anecdotal evidence suggests that light adults are killed more often by goshawks *Accipiter gentilis* than expected by their frequency in the population (Krüger et al. 2001). We predict this pattern to emerge more clearly in future years because the number of Eurasian eagle owls in the study area is currently rising after several decades of absence.

Intraspecific aggression depended not only on the breeding pair's morph but also on that of the buzzard dummy. Whereas the intermediate morph's highest fitness and occupation of the most sought-after territories (Krüger 2002b) led us to expect that its members would defend their territories most vigorously, the results showed a more complex pattern. Territory defense increased with the similarity between the morph of the defender and the "intruder," resulting in highest aggression when the dummy was of the same morph as the territory owner in 2 of the 3 morphs. Aggression has been shown to be highest when opponents are of similar competitive ability and/or the resource they compete for is of similar value to each of them (Austad 1983). In our experiment, either could be the case: the differences in aggression toward the eagle owl dummy suggest that competitive ability may vary more between than within morphs. Additionally, there are 2 factors that might represent a similar resource value to competitors of the same morph: the territory itself and the partner of the individual defending it. Buzzards mate assortatively (Krüger et al. 2001); therefore, a paired buzzard might

perceive a competitor of its own morph as the most threatening one. Similarly, territories may be of more similar value to buzzards of the same morph, as morphs seem to prefer slightly different nest sites, with dark and intermediate pairs overlapping least in their territory characteristics (Boerner 2005). Although we cannot distinguish between mate and territory defense, the latter seems the more important one as buzzards rarely change partners (Cramp and Simmons 1980) and because territories seem the more limited resource than breeding partners during the study period. Each year many individuals remained unpaired as floaters. As both territory defense and fighting over partners are done by male buzzards, the sex of the dummies (male) should have had little confounding effect on either behavior.

For a buzzard to assess a rival's most likely competitive ability, preference of partner, and/or territory by comparing the rival's morph to its own, it would require information about the latter. There are at least 2 potential mechanisms for this: innate knowledge via genetic mechanisms or learning via imprinting. The latter has already been suggested to explain assortative mating in the common buzzard (Krüger et al. 2001). Buzzard chicks are more likely to imprint on their mother's morph as she remains at the nest during the early nestling stages, whereas the male visits it mainly for deposition of food. Mother's morph explains the aggression patterns toward conspecifics better than the morph of the territory holder itself: Dark buzzards react strongest toward the intermediate dummy, followed by the dark dummy but show hardly any reaction toward the light dummy. Similarly, dark buzzards are more likely to have been raised by an intermediate mother than by a dark mother: Over the 18 years of the study, 73.3% of dark chicks had intermediate mothers, compared with only 26.7% which had dark mothers. No dark individual with a mother from the light morph has been found. This distribution can be explained by the low breeding success of dark individuals, their rarity in the population, and the inheritance pattern of the polymorphism, which follows simple Mendelian rules for a single locus with 2 alleles, assuming that intermediates are the heterozygous morph (Krüger et al. 2001). The same overlap of aggression rank and probability of mother's morph occurs in the intermediate and the light morphs (compare Figure 3): intermediates most likely descend from intermediate mothers (76.4%), followed by light and dark mothers (16% and 7.6%, respectively). Of the light individuals, 53.7% have light and 46.3% intermediate mothers, and no light chicks with dark mothers have ever been found. However, as no experimental evidence exists for self-recognition via imprinting, it remains a hypothesis worthwhile of testing.

Overall, our results show that the description of the common buzzard's polymorphism as a "plumage color polymorphism" may be an oversimplification. The marked differences between the morphs in behavior (this study), habitat preference (Boerner 2005), and parasite load (Chakarov et al. 2008) strongly suggest the presence of physiological differences between them, which go beyond plumage color. Identifying these differences and their effects on life-history trade-offs in buzzards and testing other species for similar differences will be crucial to fully understand the extent and evolutionary stability of polymorphism.

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