



CHICAGO JOURNALS



The University of Chicago

Melanin-Specific Life-History Strategies.

Author(s): Guillaume Emaresi, Pierre Bize, Res Altwegg, Isabelle Henry, Valentijn van den Brink, Julien Gasparini, and Alexandre Roulin

Source: *The American Naturalist*, Vol. 183, No. 2 (February 2014), pp. 269-280

Published by: [The University of Chicago Press](http://www.press.uchicago.edu) for [The American Society of Naturalists](http://www.asn.org)

Stable URL: <http://www.jstor.org/stable/10.1086/674444>

Accessed: 26/01/2014 04:50

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Melanin-Specific Life-History Strategies

Guillaume Emaresi,¹ Pierre Bize,^{1,2} Res Altwegg,^{3,4} Isabelle Henry,¹ Valentijn van den Brink,¹ Julien Gasparini,⁵ and Alexandre Roulin^{1,*}

1. Department of Ecology and Evolution, Biophore Building, University of Lausanne, 1015 Lausanne, Switzerland; 2. Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, United Kingdom; 3. South African National Biodiversity Institute, P/Bag X7, Claremont 7735, South Africa; 4. Animal Demography Unit, Department of Biological Sciences and Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa; 5. Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, CNRS Unité Mixte de Recherche 7625, 7 quai St-Bernard, 75252 Paris, France

Submitted June 4, 2013; Accepted August 21, 2013; Electronically published December 10, 2013

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.vq542>.

ABSTRACT: The maintenance of genetic variation is a long-standing issue because the adaptive value of life-history strategies associated with each genetic variant is usually unknown. However, evidence for the coexistence of alternative evolutionary fixed strategies at the population level remains scarce. Because in the tawny owl (*Strix aluco*) heritable melanin-based coloration shows different physiological and behavioral norms of reaction, we investigated whether coloration is associated with investment in maintenance and reproduction. Light melanic owls had lower adult survival compared to dark melanic conspecifics, and color variation was related to the trade-off between offspring number and quality. When we experimentally enlarged brood size, light melanic males produced more fledglings but in poorer condition, and they were less often recruited in the local breeding population than those of darker melanic conspecifics. Our results also suggest that dark melanic males allocate a constant effort to raise their brood independently of environmental conditions, whereas lighter melanic males finely adjust reproductive effort in relation to changes in environmental conditions. Color traits can therefore be associated with life-history strategies, and stochastic environmental perturbation can temporarily favor one phenotype over others. The existence of fixed strategies implies that some phenotypes can sometimes display a “maladapted” strategy. Long-term population monitoring is therefore vital for a full understanding of how different genotypes deal with trade-offs.

Keywords: life-history strategies, melanin, color polymorphism, genetic variation, melanin-based coloration.

Introduction

The way individuals deal with trade-offs imposed by resource limitation and biotic interactions between predators and competitors is constrained by intrinsic individual-specific genetic (Lynch 2007) and physiological properties (Lancaster et al. 2008). In such circumstances, individuals

cannot simultaneously maximize all life-history traits (MacArthur and Wilson 1967; Stearns 1989) but have to deal with trade-offs in an adaptive way depending on prevailing environmental and social conditions (Pianka 1970). One classic example is the effect of seasonality in temperate zones, causing fluctuations in the availability of resources and occurrence of stressful factors such as low ambient temperatures during winter. In contrast, in the tropical zones resources are less abundant but more homogeneously available through time and space. These contrasting ecological conditions promote the evolution of whole series of physiological traits (e.g., metabolic, hormonal, immunity), resulting in fast and slow paces of life in the temperate and tropical zones, respectively (Dobzhansky 1950; Sæther 1988; Promislow and Harvey 1990; Wiersma et al. 2007; Reale et al. 2010). Such adaptive life-history strategies have been mainly studied across species or populations of the same species (Sæther 1988; Rushton 2004) but only rarely among genotypes living in the same population (Gross 1985; Sinervo and Lively 1996; Sinervo et al. 2000; Vercken et al. 2007). These strategies rely on the two most important life-history trade-offs, namely, reproduction versus survival and offspring number versus quality (Stearns 1989). For instance, one genotype may favor reproduction over survival and in turn offspring number over quality, whereas another genotype may adopt the opposite strategy, namely maintenance over reproduction and hence offspring quality over number.

The long-lived color polymorphic tawny owl (*Strix aluco*) is a prime model species to investigate whether genotypes (identified by heritable coloration) differently deal with life-history trade-offs. This species exhibits a continuous inter-individual variation in melanin-based coloration (i.e., from light to dark reddish melanic), for which the expression is under strong genetic control and is not or is only weakly sensitive to environmental conditions (Brommer et al. 2005; Gasparini et al. 2009a; Emaresi et al. 2013). Importantly,

* Corresponding author; e-mail: alexandre.roulin@unil.ch.

studies performed in various countries have reported color-specific norms of reaction to reproductive (Roulin et al. 2011) and rearing conditions (Roulin et al. 2008), food supply (Piault et al. 2009), pathogens (Gasparini et al. 2009a, 2009b; Karell et al. 2011a), and climatic conditions (Karell et al. 2011b), leading to differences in the lifetime production of recruits (Brommer et al. 2005) and the probability of skipping reproduction (Roulin et al. 2003). These genotype-by-environment ($G \times E$) interactions may highlight the evolution of color-specific (i.e., genotype-specific) strategies to deal with life-history trade-offs. In females for instance, melanin-based coloration covaries with offspring growth rate; dark melanic foster and genetic mothers producing nestlings in better condition than light melanic mothers (Roulin et al. 2004). Given their aptitude to cope with stressful reproductive conditions (Roulin et al. 2003, 2008; Piault et al. 2009; Roulin et al. 2011), evolution may have favored light melanic owls to produce offspring that were numerous but of poorer quality, potentially explaining the observed lower parental care per nestling (i.e., higher rate of nest predation; Da Silva et al. 2013). In contrast, dark melanic owls breed more regularly (Roulin et al. 2003), and their offspring grow particularly well under prime rearing conditions (Roulin et al. 2008; Piault et al. 2009). These characteristics should lead them to produce a limited number of offspring, but of higher quality, which induces higher parental care per nestling (lower rate of nest predation; Da Silva et al. 2013) but enables the allocation of sufficient resources for maintenance traits such as immunocompetence (Gasparini et al. 2009a, 2009b) and in turn survival (Karell et al. 2011b).

In this study, we tested how differently colored individuals deal with the life-history trade-off between offspring number and quality (i.e., body mass and recruitment) as well as between reproductive effort and survival. To this end, we monitored a Swiss population of tawny owls during eight consecutive years while experimentally manipulating brood sizes of differently colored individuals to modify effort in parental care (Roulin et al. 2011) enlarged or reduced brood in terms of offspring number and quality as well as survival from one year to the next. This experiment was repeated for 6 years to investigate whether rearing experimentally enlarged (or reduced) broods over consecutive years increases the likelihood to detect color-specific life-history strategies.

Methods

Study Organism

The tawny owl is a territorial predator that breeds in Eurasian forests. It is monogamous, produces one brood per year, is highly philopatric, and can live for up to 20 years

(Galeotti 2001). This owl is relatively resistant to harsh winters and can start to breed in January. Sex roles in reproduction are clearly defined, with the mother incubating the eggs, brooding the offspring, distributing food among the progeny, and protecting the nest against predators (Da Silva et al. 2013). The male parent hunts most prey items delivered to the brood. Nestlings leave their nest at 25–30 days of age, usually before they are fully able to fly. Plumage varies from light to dark reddish, a non-sexually dimorphic trait (Emaresi et al. 2011). In contrast, there is a pronounced sexual size dimorphism with females being on average 5%–10% larger and 20%–25% heavier than males (Glutz von Blotzheim 1980).

General Method

We monitored a tawny owl population between 2005 and 2011 within a 911-km² study area in western Switzerland, where we installed 366 nest boxes in forest patches of at least 4,000 m²; the minimum distance between two nest boxes was 627 m. These managed forest patches are located at a mean altitude of 672 m (range: 458–947 m) and are composed mainly of beeches (*Fagus sylvatica*), oaks (*Quercus* spp.), and pure spruce (*Picea abies*; Roulin et al. 2011). Between 2005 and 2011, we monitored all nest boxes and found 694 clutches (138 breeding pairs in 2005, 57 in 2006, 128 in 2007, 91 in 2008, 72 in 2009, 149 in 2010, and 59 in 2011). Overall, 548 of these 694 clutches generated at least one hatchling (79.0%), while 436 broods produced at least one fledgling (62.8%). Clutch size varied between one and eight eggs (mean \pm SD = 3.78 ± 1.51 eggs), laid between February 18 and May 29 (mean \pm SD = April 6 ± 16 days). When considering nests where at least one egg hatched, 71% of the eggs hatched. The mean number of fledglings per brood was 2.1 ± 2.04 .

Assessment of Plumage Coloration

The tawny owl has heterogeneous plumage color patterns that vary continuously in the degree of reddishness (Gasparini et al. 2009a). Variation is so pronounced (see pictures in Da Silva et al. 2013) that we visually scored adult plumage coloration in the field on the basis of five distinct color categories (1 = reddish, 2 = reddish brown, 3 = brown, 4 = brown gray, 5 = gray; Roulin et al. 2005). Because we recently found that a so-called gray coloration reflects an absence of melanin pigments stored in feathers, the scale we used in previous articles is a bit counterintuitive (a larger score indicates a lower degree of melanin). To obtain a more intuitive scale from light to dark melanic, we multiplied the above color scores by -1 . The scoring was also consistent regardless of which biologist was doing it, as evidenced by high interannual repeatability

of color scores visually assigned to the same individuals between 2005 and 2011 ($r = 0.89 \pm 0.02$, $F_{174,383} = 13.76$, $P < .0001$). Here it is noteworthy that visual scores were strongly correlated with color measurements performed with a spectrophotometer (Pearson's correlation: $r = -0.80$, $n = 302$, $P < .0001$). Visual scoring into categories takes into consideration the whole plumage coloration, and this approach is therefore more representative of bird coloration than measuring it on the basis of a couple of back feathers (Brommer et al. 2005; Vercken et al. 2008). As we have already demonstrated elsewhere that birds do not change coloration at adulthood in any consistent way (Roulin et al. 2003), we calculated a mean color score value for individuals that were captured and color scored on several occasions during the entire study period (median is 2 captures and scoring per individual, range 1–13). All the statistical analyses were performed using this individual mean visual score which can be considered as a continuous variable (see fig. 2 in Da Silva et al. 2013; Emaresi et al. 2011).

Experimental Procedure

Out of the 694 clutches monitored between 2005 and 2011, 388 broods were matched into pairs according to similar hatching dates (Pearson's correlation, $r = 0.92$, $P < .0001$). We manipulated brood size by exchanging on average two hatchlings or eggs from a so-called enlarged nest against three hatchlings or eggs from a so-called reduced nest. Initial clutch sizes of enlarged and reduced nests were on average similar (Student's t -tests; $t_{1,272} = 1.43$, $P = .15$). We successfully generated broods with a different number of nestlings as more individuals fledged from enlarged than reduced broods (mean \pm SD, 3.95 ± 1.92 vs. 2.55 ± 1.61 , respectively; Student's t -test: $t_{1,270} = -6.44$, $P < .0001$). We captured 274 female parents during incubation or just after hatching and 252 male parents when their offspring were 10–15 days of age. The probability of capturing males was independent of the brood size manipulation treatment (logistic regression: $\chi^2 = 0.79$, $df = 1$, $P = .51$). To estimate nestling growth, nestlings were recaptured every 5 days until they left the nest at 25–30 days of age (mean number of captures per individual \pm SD = 5.0 ± 1.2). On capture, individuals were weighed to the nearest gram, their left wing length was measured to the nearest 1 mm and their left tarsus to the nearest 0.1 mm. Adult wing and tarsus lengths were not associated with plumage coloration (Pearson's correlations, P values $>.47$).

Plumage coloration, wing and tarsus lengths of breeding adults (197 males and 193 females) did not differ significantly between the two brood size treatments (Student's t -tests, P values $>.08$). Within each pair of nests, foster

and biological parents did not significantly resemble each other with regard to coloration (females: $r = -0.02$, $P = .84$; males: $r = -0.16$, $P = .09$), while intranest pairing with respect to coloration was not assortative in both treatments (Pearson's correlations; reduced nests: $r = 0.01$, $n = 116$, $P = .95$, enlarged nests: $r = 0.01$, $n = 126$, $P = .94$).

Statistical Procedures

Using our long-term data set of population monitoring, we examined whether tawny owls showed color-specific survival rates, based on capture-mark-recapture techniques (Lebreton et al. 1992). This approach accounts for the fact that individuals may not have been captured in years when they were in fact alive. Our starting model was the classic Cormack-Jolly-Seber model with time-dependent survival and recapture probabilities for male and female tawny owls. We first simplified the basic structure of this model and selected the most parsimonious structure based on the sample-size-adjusted Akaike Information Criterion (AIC_c). We then included color score as a time-constant individual covariate and treatment (enlarged, reduced, or not manipulated) as a time-varying individual covariate in the model. We also examined possible interactions between tawny owl coloration and brood size treatment and the three-way interaction between sex, coloration, and treatment. When considering only the manipulated broods, we obtained similar results (not shown). Finally, we examined whether treatment in the previous year had an effect on current survival and whether this interacted with the current brood size treatment, to see whether sustained exposure to one treatment had particularly large effects. All models were fitted in MARK 6.0 (White and Burnham 1999).

Out of the 388 experimentally manipulated broods, 274 produced fledglings. We were able to capture both breeding adults for 252 broods. In five cases, male captures potentially led to nestling desertion, constraining us to exclude these broods from the statistical analyses. To examine how differently colored birds deal with the trade-off between offspring number and quality, we considered a subset of 235 broods producing at least one fledgling and 12 predated broods. We still considered predated broods in our analyses since nest defense behavior is likely to be involved in key life-history trade-offs (Montgomerie and Weatherhead 1988; Wolf et al. 2007), and since the intensity of nest defense behavior is correlated with coloration in the tawny owl (Da Silva et al. 2013; see also Emaresi et al. 2011). To test whether plumage coloration of the rearing parents was associated with variation in fledgling production, we performed a linear mixed-model ANCOVA including the number of fledglings as dependent

variable and year and identity of the male that reared the brood as two random factors. Hatching date of the first egg and brood size before manipulation were introduced as covariates in the model, while brood size manipulation treatment and coloration of the parents that reared the brood were entered as independent variables, plus all possible interactions between the latter three variables. Since raising an enlarged brood over several consecutive years may have devastating long-term effects on reproductive success, we considered males for which we manipulated their brood in two successive years. We performed a linear mixed-model ANCOVA including the number of fledglings in the second breeding year as dependent variable and year and male identity as two random factors. Using hatching date of the first egg and brood size before manipulation in the second breeding year as covariates, we introduced class of successive brood size manipulation treatments in year X_1 and year X_2 (i.e., enlarged-enlarged; reduced-reduced; enlarged-reduced and reduced-enlarged) and rearing male coloration as independent variables, plus the two-way interaction between both variables.

To investigate color-specific variation in offspring quality, we performed a linear mixed-model ANCOVA including nestling body mass measured just before fledging (i.e., at a mean \pm SD age of 26 ± 3 days) as dependent variable and year and brood identity as two random factors. Note that it was not possible to measure all nestlings at exactly the same age because within the same brood there is variation in age due to hatching asynchrony (mean age difference between two nest mates was 1.8 days). We introduced time of the day when nestlings were captured, nestling wing length, and nestling sex as covariates. We entered brood size manipulation treatment, coloration of the rearing male and rearing female, plus all possible interactions between these three variables as independent variables. In another similar model, we examined whether a relationship between nestling body mass and parental coloration differed between cross-fostered and non-cross-fostered individuals.

Finally, we tested whether the proportion of fledglings that were recruited as breeders in the local population in following years covaried with plumage coloration of the rearing father and mother. We used a generalized linear mixed model with a binomial error structure and logit link, considering the number of recruits from a brood as the dependent variable and the number of fledglings from the same brood as the binomial denominator. Year and male identity were entered as two random variables, mean nest mate body mass and hatching date were introduced as covariates, and brood size manipulation and coloration of the rearing father and mother were entered as independent variables, plus the two-way interaction between both variables. To investigate the relationship between re-

cruitment probability and melanin-based coloration, we tested whether natal dispersal between the nest where an individual fledged and the nest where it bred for the first time was associated with its own coloration or the coloration of its parents. We had a sample of 131 recruits raised in experimentally enlarged ($n = 76$) or reduced ($n = 55$) broods. Natal dispersal distance varied between 0.75 and 23.63 km (mean is 5.12 km).

For each linear mixed-effects model, we ran full factorial models and then dropped nonsignificant terms (starting with nonsignificant interactions) in a stepwise manner in order to produce minimum adequate final models. Note that all significant terms in the final model were already significant before removing nonsignificant terms. Statistical tests were two-tailed, and significance level was set to .05. Mother identity was entered as a random variable in preliminary models, but as maternal coloration did not account for variation in breeding parameters, we removed it from final models. Clutch size, brood size at fledging, and nestling body mass followed a normal distribution. In all models, residuals were normally distributed and variances were homogeneous between treatments. Linear mixed models were performed using JMP IN 8.0 and generalized linear mixed models in R, version 2.12 (Comprehensive R Archive Network).

Results

Color-Specific Survival

According to the most parsimonious model structure that kept survival constant across sexes and years and allowed the recapture rates to vary over the years and between the sexes (model 7, table 1), survival was 0.69 (SE = 0.02). Adding color scores to this model resulted in a better fit, indicating that darker melanic owls survived better than lighter melanic ones (models 1–3, table 1; fig. 1). We found no evidence that the brood manipulation experiment affected survival, either directly (model 4, table 1) or through interactions with color or sex (models 5 and 8, table 1).

Color-Specific Reproductive Success

The effect of paternal (but not maternal) coloration on the number of fledglings differed significantly between enlarged and reduced broods (model A, table A1; tables A1–A4 available online, $F_{1,238.5} = 4.57$, $P = .034$). In enlarged broods, lighter melanic fathers produced significantly more fledglings than darker melanic ones (model B, table A1; $F_{1,88.34} = 5.13$, $P = .026$), while in the reduced treatment, the number of fledglings was not significantly associated with paternal coloration (model C, table A2; $F_{1,95.77} = 1.07$, $P = .30$; fig. 2).

Table 1: Capture-mark-recapture models of annual survival in relation to melanin-based coloration and experimental brood size manipulation treatments in adult tawny owls

Model	ΔAIC_c	Akaike weights	K	Deviance
1. φ (col)P(year+sex)	.000	.361	9	1,471.54
2. φ (sex \times col)P(year+sex)	.586	.269	11	1,468.01
3. φ (sex+col)P(year+sex)	.938	.226	10	1,470.42
4. φ (col+treat)P(year+sex)	3.215	.072	11	1,470.64
5. φ (sex \times col \times treat)P(year+sex)	5.460	.024	19	1,456.21
6. φ ()P(year+sex+col)	6.327	.015	9	1,477.87
7. φ ()P(year+sex)	6.924	.011	8	1,480.51
8. φ (col \times treat)P(year+sex)	7.110	.010	13	1,470.4
9. φ (sex)P(year+sex)	7.919	.007	9	1,479.46
10. φ (sex)P(year)	9.280	.003	8	1,482.87
11. φ (year \times sex)P(year)	17.072	.000	17	1,472.02
12. φ (year \times sex)P(year \times sex)	22.538	.000	22	1,466.94

Note: The models consisted of parameters modeling survival (φ) and those modeling recapture probabilities (P). We examined the effects of year, sex, coloration (col) and brood size treatment (treat), either as main effects only (symbolized by a plus sign) or as main effects and interactions (\times). The different treatments were brood size enlargement, reduction, or not manipulated, which were entered as time-varying covariates. Broods of owls that were not captured were not manipulated. Model selection was based on Akaike's Information Criterion (AIC_c); Akaike weights give the relative support a particular model has in relation to the others; and K is the number of estimated parameters.

When we considered males for which we manipulated the size of their brood in two successive years, the interaction between the category of successive treatments (i.e., reduced-reduced, reduced-enlarged, enlarged-reduced, enlarged-enlarged) and paternal coloration on the number of fledglings produced in the second year was highly significant (model A, table A2; $F_{3,12.97} = 7.61$, $P = .003$). Lighter melanic males produced significantly more fledglings than darker melanic ones after having raised an enlarged brood in two consecutive years (model B, table A2; $F_{1,6.376} = 20.75$, $P = .003$; fig. 3), while the opposite was true when raising a reduced brood in two consecutive years (model C, table A2; $F_{1,5.454} = 11.55$, $P = .017$; fig. 3). Whatever the brood size treatment, darker melanic males produced consistently two or three fledglings, whereas light melanic males produced about 1 fledgling when brood was experimentally reduced and five when enlarged (fig. 3).

Color-Specific Offspring Body Mass

We detected a significant interaction between the brood size manipulation experiment and coloration of the rearing father on fledging body mass (table A3A; $F_{1,226.5} = 10.40$, $P = .001$). This effect was independent of nestling origin (i.e., the "cross-fostered" factor was not significant, alone or in interaction with coloration of foster father and/or the brood size manipulation, P values $>.10$; model not shown). In the same model, maternal coloration was not significant alone or in interaction with brood size manip-

ulation experiment and paternal coloration (P values $>.14$, table A3A). In the enlarged treatment, darker melanic males produced fewer offspring that were heavier than those produced by lighter melanic males ($F_{1,106.1} = 4.11$, $P = .045$), whereas no relationship between offspring body mass and paternal coloration was detected in the reduced treatment (fig. 4; table A3B, A3C; $P = .57$).

Color-Specific Recruitment Rate

We further investigated the links between paternal coloration, offspring condition at fledging and recruitment of those offspring raised in either reduced or enlarged broods. We tested whether the likelihood of being recruited in the local breeding population is associated with parental coloration, offspring condition, or treatment entered in the same model. Accordingly, we found a significant interaction between brood size manipulation experiment and coloration of the rearing male on the proportion of offspring per brood recruited as breeders in the local population in following years, independently of the mean offspring body mass (model A, table A4; $z = 2.42$, $P = .016$). Nestlings raised by dark melanic males were more frequently recruited when experiencing an experimentally reduced brood (model B, table A4; $z = 2.41$, $P = .016$), whereas in the enlarged treatment there was no relationship between paternal coloration and the probability of producing at least one recruit (model C, table A4; $z = -0.37$, $P = .71$). This outcome is not a consequence of

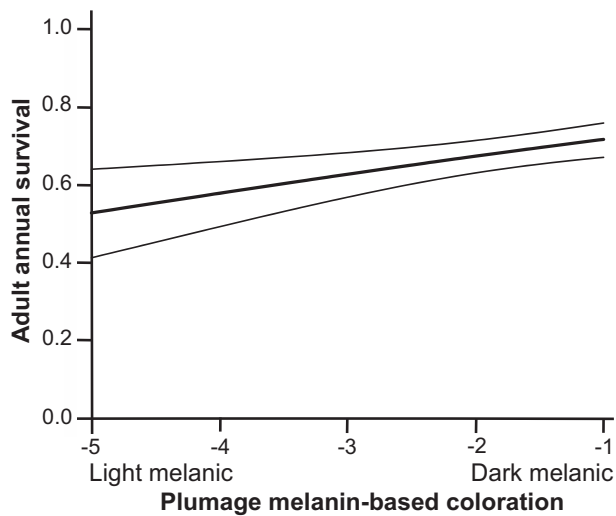


Figure 1: Adult annual survival rate in relation to melanin-based plumage coloration in the tawny owl. Survival estimates are derived from capture-mark-recapture techniques (model 1 in table 1).

color-specific dispersal behavior, since the dispersal distance per recruited fledgling (i.e., distance between nest of fledging and nest of recapture as breeding adult) was independent of paternal coloration (linear mixed model with brood identity and year as two random variables; paternal coloration: $F_{1,63.84} = 1.22$, $P = .27$; brood size manipulation: $F_{1,66.21} = 0.55$, $P = .46$; interaction: $F_{1,65.41} = 0.20$, $P = .66$; controlling for nestling sex: $F_{1,112.2} = 0.61$, $P = .44$). Replacing paternal coloration by recruit coloration did not modify our conclusion; that is, there was no effect of offspring coloration on their dispersal distances. It is notable that, because in our analysis we considered only nests that produced at least one fledgling, this result cannot be explained by a lower predation rate in nests raised by darker melanic males (Da Silva et al. 2013).

Discussion

Evolutionary biologists usually consider that intra- and interpopulation variation in the degree of coloration is due to the expression of coloration being condition dependent (Rowe and Houle 1996). Therefore, we need a mechanism to explain the evolutionary stability of color traits for which the interindividual variation is almost purely accounted by genetic factors as in the tawny owl (Emaresi et al. 2013). Pigmentation often covaries with life-history traits (Roulin 2004; McKinnon and Pierotti 2010) but whether it is associated with the way individuals deal with life-history trade-offs is usually unknown or suspected (Vercken et al. 2007) but rarely demonstrated (Sin-

ervo et al. 2000). This is, however, a key issue as it could explain how heritable variation in traits used in various contexts, including intraspecific communication and predator-prey interactions, can remain evolutionary stable. If dealing with life-history trade-offs is sensitive to the environment in a color-specific way, these norms of reaction or genotype-by-environment interaction could account for spatiotemporal variation in genetically determined coloration.

Color-Specific Reproductive Strategies

We examined in the tawny owl the association between variation in the degree of melanin-based pigmentation,

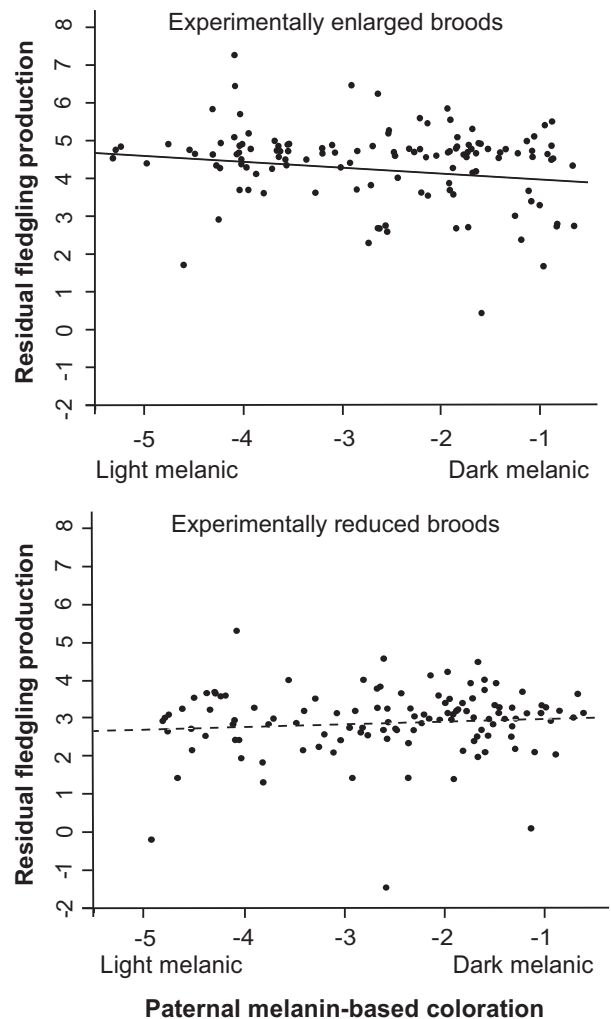


Figure 2: Residual fledging production in relation to paternal melanin-based coloration in experimentally enlarged and reduced broods in the tawny owl. Values are derived from models B and C of table A2, available online. Significant linear regressions are illustrated by straight regression lines, whereas nonsignificant linear regressions are illustrated by dashed regression lines.

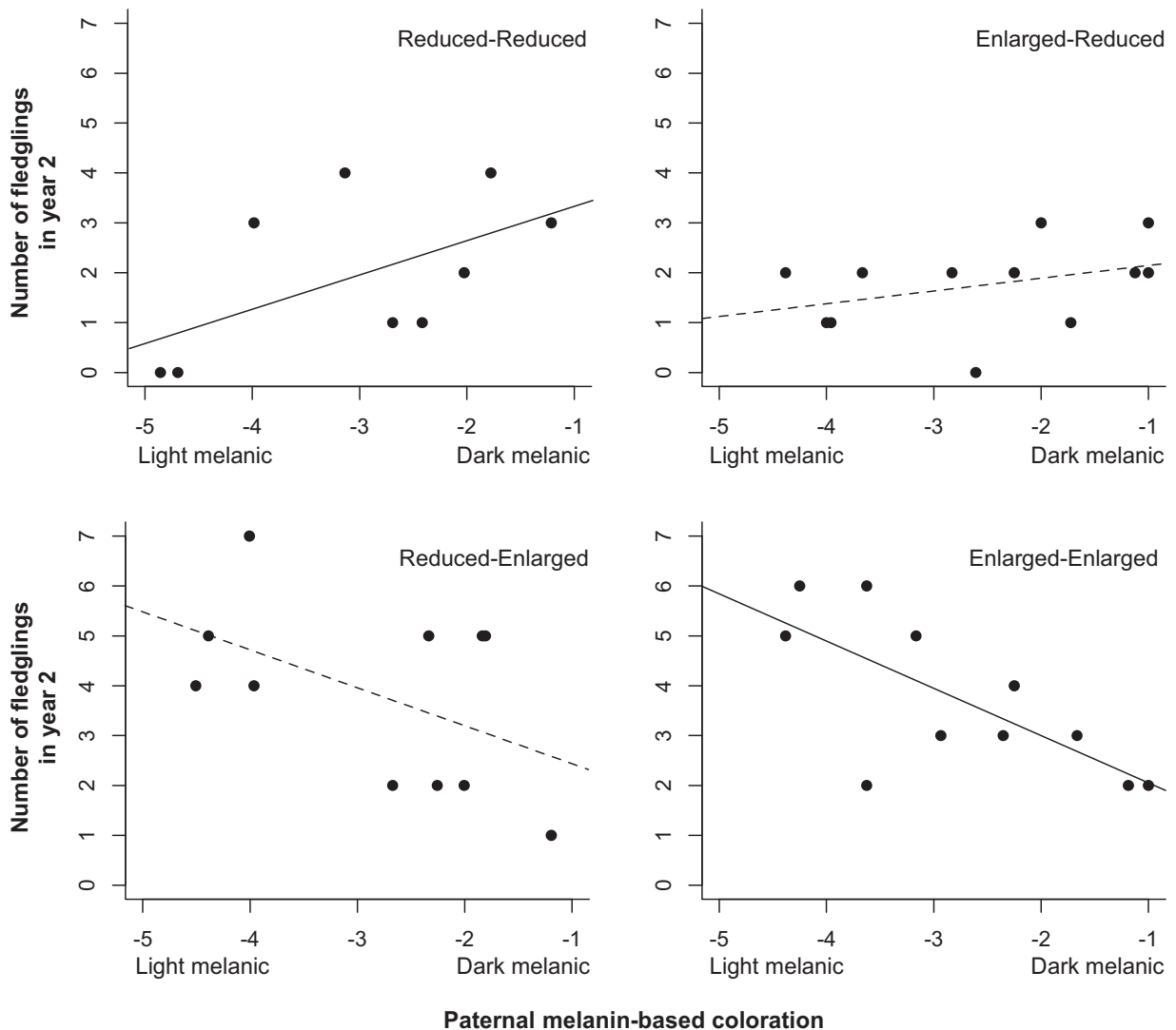


Figure 3: Number of fledglings in relation to melanin-based coloration of the father and brood size manipulation experiment in the tawny owl. We considered number of fledglings produced after 2 years of having manipulated brood size for the same breeding males. Enlarged-Enlarged: number of fledglings in year 2 for males with their brood size enlarged in years 1 and 2 (linear regression, $n = 10$, $P = .003$); Reduced-Reduced; with their brood size reduced in years 1 and 2 (linear regression, $n = 9$, $P = .017$); Reduced-Enlarged: with their brood size reduced in year 1 and enlarged in year 2 (linear regression, $n = 11$, $P = 0.24$); and Enlarged-Reduced: with their brood size enlarged in year 1 and reduced in year 2 (linear regression, $n = 12$, $P = .89$). Significant linear regressions are illustrated by straight regression lines, whereas nonsignificant linear regressions are illustrated by dashed regression lines.

survival, and several measures of reproductive success. Compared to light melanic males, darker-colored males had higher survival but produced fewer offspring in experimentally enlarged broods. Yet, these offspring were in better condition than offspring of light melanic males and were more often recruited as breeder in the local population.

Lighter melanic males better coped with two consecutive energy-demanding breeding seasons than darker melanic males (i.e., they produced more offspring in experimen-

tally enlarged broods), while darker melanic males better managed two consecutive reduced broods than lighter melanic males (i.e., they produced more offspring in experimentally reduced broods). Dark melanic males produced around three fledglings in the two brood size treatments, whereas light-colored males raised about one fledgling in reduced broods but five to six in enlarged broods (see fig. 3). This supports the idea (Roulin et al. 2011) that dark melanic owls adopt a rather constant reproductive strategy independently of environmental conditions by investing a

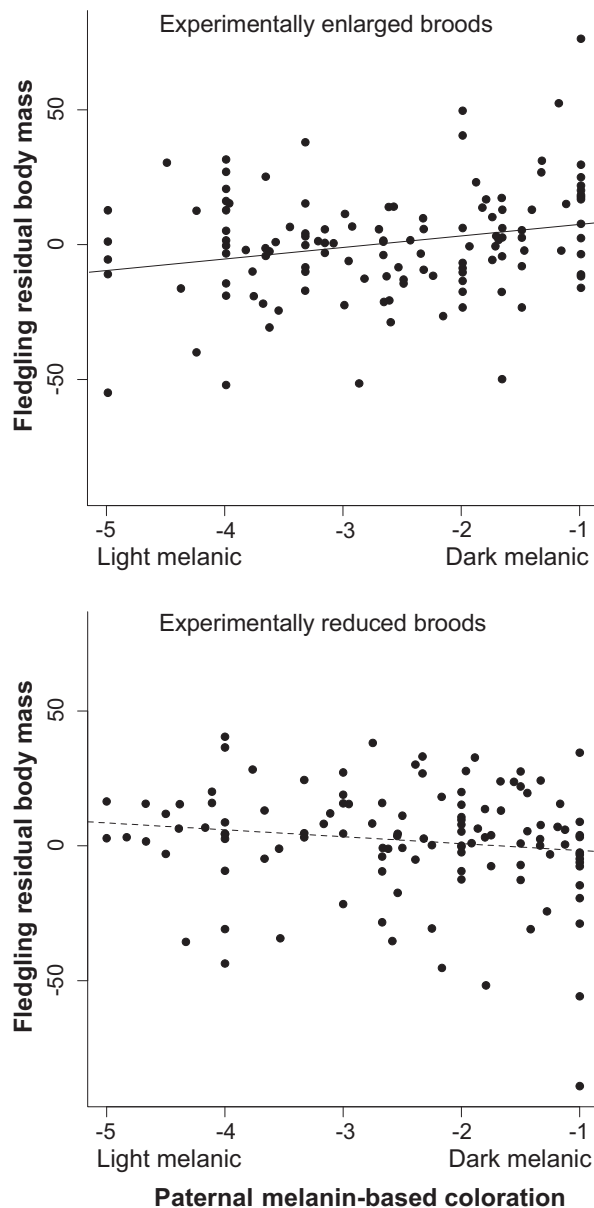


Figure 4: Fledging body mass in relation to paternal melanin-based coloration and brood size manipulation experiment in the tawny owl. For this graph, but not for the analyses, we calculated mean offspring body mass for each adult male, while controlling for nestling sex, wing length, time of the day, and year (i.e., residual body mass). The relationship is significant in experimentally enlarged broods (Pearson's correlation: $r = -0.23$, $n = 123$ different males, $P = .008$) but not in experimentally reduced broods ($r = 0.10$, $n = 115$ different males, $P = .28$). Significant linear regressions are illustrated by straight regression lines, whereas nonsignificant linear regressions are illustrated by dashed regression lines.

fixed effort to raise a given number of offspring whatever the initial size of their clutch. In contrast, light melanic owls adopt a flexible strategy by producing more offspring than dark melanic owls when conditions permit (i.e., enlarged-enlarged treatment in fig. 3). The potential coexistence of generalists that adopt a flexible strategy and of specialists that adopt a fixed strategy (Svanback and Schluter 2012) suggests genetic variation in life-history reaction norms associated with melanin-based coloration (see fig. 5 in Roulin and Ducrest 2013). Such genetic variation has been demonstrated in some organisms (e.g., Hutchings et al. 2007; van de Pol 2012) and raises a number of issues regarding how variation in reaction norms can evolve and be evolutionary stable. For instance, de Jong and Gavrillets (2000) found that genetic variation in reaction norms is higher in environments that are less variable. It would be interesting to examine whether variation in coloration is more pronounced in tawny owl populations living in homogeneous environments compared to those in heterogeneous environments. This is an important issue as the coexistence of specialists and generalists in the same population is usually considered to be restricted to some specific ecological conditions (Egas et al. 2004).

The hypothesis that light-colored individuals finely adjust their investment in reproduction in relation to environmental conditions, whereas dark individuals maintain a constant effort implies that they should also differ in a suite of behavioral, ecological, and physiological attributes (Ricklefs and Wikelski 2002; Reale et al. 2010). Accordingly, we found that light-colored females reduced their levels of the POMC prohormone (precursor of the pleiotropic melanin-stimulating hormone that triggers the production of eumelanin and many other phenotypes; Ducrest et al. 2008) when we experimentally enlarged their brood while dark melanic females did not modify their hormone levels (Roulin et al. 2011). The finding that dark melanic tawny owls have a higher survival prospect than lighter conspecifics (fig. 1) implies that differently colored individuals should differentially allocate resources among life-history traits (MacArthur and Wilson 1967; Pianka 1970; Mcleod et al. 1981; Stearns 1992). Given the pattern of color-specific survival (which was independent of the brood size manipulation experiment), we would predict that darker melanic owls favor offspring quality over number (Pianka 1970). In line with this prediction, differently colored male tawny owls did not deal with the trade-off between offspring number and quality in a similar way. Dark melanic males produced fewer but higher-quality offspring that were more often recruited in the local breeding population than offspring of lighter melanic males. Interestingly, the production of higher-quality offspring by darker males was detected in the two brood size treatments

but not for the same fitness offspring trait. When brood size was experimentally enlarged darker melanic males produced heavier offspring than lighter melanic males; when we experimentally reduced broods darker melanic males produced more recruits independently of body mass than lighter melanic males. This suggests that darker melanic males are able to produce higher-quality offspring with respect to alternative phenotypic traits in different environments.

In our population, the fine-tuned investment in reproduction related to breeding conditions by lighter melanic males does not appear to be the best strategy, since darker melanic males produced more recruits and showed higher survival, a situation that may differ between populations. For instance, in a Finnish population lighter melanic males achieved a higher fitness (Brommer et al. 2005). In Switzerland, the strategy adopted by light-colored males was to produce a larger number of offspring, but this did not result in more recruits. Although light melanic males have a lower survival than darker melanic conspecifics, this was apparently not because they invest more effort in reproduction, since color-specific survival was independent of the brood size manipulation experiment (this study) and since they reproduce less often than darker melanic conspecifics (Roulin et al. 2003). A possible explanation for this result is that light melanic males are not well adapted to the environmental conditions currently prevailing in our population (a similar situation as found in the color polymorphic common buzzard *Buteo buteo*; Krüger et al. 2001). This interpretation may explain why we already found that light-colored tawny owls invest more effort to cope with various stressful factors (Roulin et al. 2003, 2008, 2011; Gasparini et al. 2009a; Piau et al. 2009). This energy-demanding strategy may allow individuals to be constantly adapted to the prevailing environmental conditions, but apparently this strategy is currently not the best one in our population. Potentially, the costs incurred by this strategy may be too high, and, as described by Ernande and Dieckmann (2004), light melanic individuals may be “jack[s] of all trades but master[s] of none.” The strategy deployed by dark melanic males by taking good care of a limited number of high-quality offspring appears to be more successful. These males invest a rather fixed budget in reproduction as shown by the fact that darker melanic birds had a higher survival independently of the brood size manipulation experiment. To conclude, darker melanic males achieve a higher fitness by surviving longer, breeding more often in a lifetime (Roulin et al. 2003), being less often depredated (Da Silva et al. 2013), and by producing heavier offspring and offspring that were more often recruited for other reasons than just because they are heavier (this study). This demonstrates that melanin-based coloration is associated with reproductive strategies

and life-history trade-offs, an important result given the increased interest among evolutionary biologists in the adaptive function of pigmentation.

Evolutionary Stability of Color Variation and the Associated Reproductive Strategies

In the tawny owl, as in other birds (Roulin 2004) and animals (Mann and Sefc 2013), variation in melanin-based coloration is often under strong genetic control. This provides an opportunity to investigate whether in different organisms a given color pattern (dark or light melanic) is associated with similar or different adaptations and to examine how color variation is evolutionary stable. In this context, the finding that darker melanic tawny owls achieve a higher fitness is consistent with two mutually exclusive scenarios. First, the polymorphism is transient with darker melanic individuals currently invading populations. This situation may frequently occur because species that display a high degree of color variation (so-called color polymorphic species) are relatively rare in animal populations (Galeotti et al. 2003), suggesting that in monochromatic species mutations encoding for a new color morph are rare or selectively neutral (or even detrimental) but only rarely advantageous. An alternative is that once a color polymorphism is established, one morph (the ancestral or derived one) performs better and thus invades the population. Second, color polymorphism is maintained by frequency-dependent selection (Losey et al. 1997; Gigord et al. 2001) or local adaptation (Kassen 2002; Bell 2010). Due to stochastic environmental perturbation there might be periods during which one phenotype temporarily achieves a higher fitness. We believe that this last scenario is the most likely because the tawny owl is color polymorphic throughout its range (Galeotti 2001). Furthermore, in a Finnish population, a short-term study showed that light-colored tawny owls achieve a higher fitness than dark melanic conspecifics (Brommer et al. 2005), whereas throughout Finland, dark melanic owls currently perform better apparently as a consequence of climate warming (Karell et al. 2011b). Therefore, our results showing that darker melanic owls produce more recruits and have a higher survival may be a transient situation that can be observed in short-term studies and reflect short-term temporal perturbation around an evolutionary equilibrium.

Although flexibility in behavior should allow organisms to finely track changes in their environment, behavioral plasticity as shown by light-colored males can entail substantial costs (DeWitt et al. 1998). Behaving optimally in any situation implies the allocation of resources by trying some suboptimal behavior, especially if there is little information about the environment. A game-theoretic

model (McElreath and Strimling 2006) demonstrated that situations where individuals have noisy information about environmental conditions, combined with differences in individual state (e.g., morphological differences such as melanin-based coloration), can lead to evolutionarily stable strategies within a single population. Depending on environmental stochasticity in habitat quality, individuals perform better by displaying alternative behaviors, especially those affecting life-history decisions. Adopting a fixed behavioral tactic, as shown by dark melanic males, can be the best solution rather than trying to predict and adapt to all situations as performed by lighter melanic conspecifics (Sih et al. 2004; Bell 2007; Wolf et al. 2007). This proposition is consistent with our findings that dark melanic males survive longer and produce more recruits than light melanic ones. Here, we suggest that different genetically inherited color variants can be maintained within populations because of temporal fluctuations in selective regimes favoring flexible or constant reproductive strategies (Hedrick 1986), induced by environmental fluctuations in food availability. There are indeed situations where producing more offspring even at the expense of quality can be favored. When the carrying capacity of a population is higher than the total number of breeding pairs, individuals may better produce more offspring to fill the unoccupied territories. In contrast when food becomes scarce, the carrying capacity of a population may drastically decrease, favoring the production of higher quality offspring at the expense of offspring number (Stearns 1992). More long-term studies are required to examine the relationship between population dynamics and fluctuations in the benefits of alternative strategies to deal with the trade-offs between offspring number and quality and between reproductive investment and self-maintenance.

Acknowledgments

We are grateful to O. Arevalo, S. Cotting, A. Da Silva, A. Dreiss, A.-L. Ducrest, E. Gonzalez, S. Joye, E. Luzio, Y. Ménétrey, M. Noll, R. Piau, P.-A. Ravussin, C. Ruppli, and D. Vuillen for assistance in the field and J. Bronstein, T. Broquet, P. Fontanillas, T. Williams, and two anonymous reviewers for useful comments on previous versions of the manuscript. This study was financially supported by the National Research Foundation of South Africa and by the Swiss National Science Foundation (PPOA-102913 and 3100AO_120517 to A.R. and PPOA-109009 and 31003A_129488 to P.B.). The study was approved by the Service vétérinaire du canton de Vaud.

Literature Cited

- Bell, A. M. 2007. Evolutionary biology: animal personalities. *Nature* 447:539–540.
- Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:87–97.
- Brommer, J. E., K. Ahola, and T. Karstinen. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society B: Biological Sciences* 272:935–940.
- Da Silva, A., V. van den Brink, G. Emaresi, E. Luzio, P. Bize, A. N. Dreiss, and A. Roulin. 2013. Melanin-based colour polymorphism signals aggressive personality in nest and territory defence in the tawny owl (*Strix aluco*). *Behavioral Ecology and Sociobiology* 67: 1041–1052.
- De Jong, G., and S. Gavrillets. 2000. Maintenance of genetic variation in phenotypic plasticity: the role of environmental variation. *Genetics Research* 76:295–304.
- DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13: 77–81.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* 38:209–221.
- Ducrest, A.-L., L. Keller, and A. Roulin. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology and Evolution* 23:502–510.
- Egas, M., U. Dieckmann, and M. W. Sabelis. 2004. Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. *American Naturalist* 163:518–531.
- Emaresi, G., P. Bize, J. Gasparini, R. Piau, and A. Roulin. 2011. Plumage polymorphism in melanin-based coloration: a case study in the tawny owl *Strix aluco*. Pages 242–252 in I. Zuberogotia and J. E. Martínez, eds. *Ecology and conservation of European forest-dwelling raptors*. Departamento de Agricultura de la Diputación Foral de Bizkaia, Bizkaia, Spain.
- Emaresi, G., A.-L. Ducrest, P. Bize, H. Richter, C. Simon, and A. Roulin. 2013. Pleiotropy in the melanocortin system: expression levels of this system are associated with melanogenesis and pigmentation in the tawny owl (*Strix aluco*). *Molecular Ecology* 22: 4915–4930.
- Ernande, B., and U. Dieckmann. 2004. The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. *Journal of Evolutionary Biology* 17:613–628.
- Galeotti, P. 2001. *Strix aluco* tawny owl. *BWP Update* 3:43–77.
- Galeotti, P., D. Rubolini, P. O. Dunn, and M. Fasola. 2003. Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology* 16:635–646.
- Gasparini, J., P. Bize, R. Piau, K. Wakamatsu, J. D. Blount, A. L. Ducrest, and A. Roulin. 2009a. Strength and cost of an induced immune response are associated with a heritable melanin-based colour trait in female tawny owls. *Journal of Animal Ecology* 78: 608–616.
- Gasparini, J., R. Piau, P. Bize, and A. Roulin. 2009b. Synergistic and antagonistic interactions between different branches of the immune system is related to melanin-based coloration in nestling tawny owls. *Journal of Evolutionary Biology* 22:2348–2353.
- Gigord, L. D. B., M. R. Macnair, and A. Smithson. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina*

- (L.) Soð. Proceedings of the National Academy of Sciences of the USA 98:6253–6255.
- Glutz von Blotzheim, U. N., and K. Bauer. 1980. Handbuch der Vögel Mitteleuropas. Vol. 9. Columbiformes-Piciformes. Akademische, Wiesbaden.
- Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47–48.
- Hedrick, P. W. 1986. Genetic polymorphism in heterogenous environments: a decade later. *Annual Review of Ecology and Systematics* 17:535–566.
- Hutchings, J. A., D. P. Swain, S. Rowe, J. D. Eddington, V. Puvannendran, and J. A. Brown. 2007. Genetic variation in life-history reaction norms in a marine fish. *Proceedings of the Royal Society B: Biological Sciences* 274:1693–1699.
- Karell, P., K. Ahola, T. Karstinen, H. Kolunen, H. Siitari, and J. E. Brommer. 2011a. Blood parasites mediate morph-specific maintenance costs in a colour polymorphic wild bird. *Journal of Evolutionary Biology* 24:1783–1792.
- Karell, P., K. Ahola, T. Karstinen, J. Valkama, and J. E. Brommer. 2011b. Climate change drives microevolution in a wild bird. *Nature Communications* 2:208, doi:10.1038/ncomms1213.
- Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* 15:173–190.
- Krüger, O., J. Lindström, and W. Amos. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* 55:1207–1214.
- Lancaster, L. T., L. C. Hazard, J. Clobert, and B. R. Sinervo. 2008. Corticosterone manipulation reveals differences in hierarchical organization of multidimensional reproductive trade-offs in *r*-strategist and *K*-strategist females. *Journal of Evolutionary Biology* 21:556–565.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Losey, J. E., A. R. Uves, J. Harmon, F. Ballantyne, and C. Brown. 1997. A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* 388:269–272.
- Lynch, M. 2007. The origin of genome architecture. Sinauer, Sunderland, MA.
- MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.
- Mann, M. E., and Sefc, K. M. 2013. Colour variation in cichlid fish: developmental mechanisms, selective pressures and evolutionary consequences. *Seminars in Cell and Developmental Biology* 24:516–528.
- McElreath, R., and P. Strimling. 2006. How noisy information and individual asymmetries can make “personality” an adaptation: a simple model. *Animal Behaviour* 72:1135–1139.
- McKinnon, J. S., and M. E. R. Pierotti. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology* 19:5101–5125.
- McLeod, M. J., D. J. Hornbach, S. I. Guttman, C. M. Way, and A. J. Burky. 1981. Environmental heterogeneity, genetic-polymorphism, and reproductive strategies. *American Naturalist* 118:129–134.
- Montgomerie, R. D., and P. J. Weatherhead. 1988. Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology* 63:167–187.
- Pianka, E. R. 1970. On *r*- and *K*-selection. *American Naturalist* 104:592–597.
- Piault, R., J. Gasparini, P. Bize, S. Jenni-Eiermann, and A. Roulin. 2009. Pheomelanin-based coloration and the ability to cope with variation in food supply and parasitism. *American Naturalist* 174:548–556.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative-analysis of life-history variation among mammals. *Journal of Zoology* 220:417–437.
- Reale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P. O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:4051–4063.
- Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. *Trends in Ecology and Evolution* 17:462–468.
- Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* 79:815–848.
- Roulin, A., P. Bize, P. A. Ravussin, and L. Broch. 2004. Genetic and environmental effects on the covariation between colour polymorphism and a life-history trait. *Evolutionary Ecology Research* 6:1253–1260.
- Roulin, A., P. Bize, N. Tzaud, M. Bianchi, P. A. Ravussin, and P. Christe. 2005. Oxygen consumption in offspring tawny owls *Strix aluco* is associated with colour morph of foster mother. *Journal of Ornithology* 146:390–394.
- Roulin, A., and A.-L. Ducrest. 2013. Genetics of coloration in birds. *Seminars in Cell and Developmental Biology* 24:594–608.
- Roulin, A., B. Ducrest, P. A. Ravussin, and R. Altwegg. 2003. Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. *Journal of Avian Biology* 34:393–401.
- Roulin, A., G. Emaresi, P. Bize, J. Gasparini, R. Piault, and A. L. Ducrest. 2011. Pale and dark reddish melanic tawny owls differentially regulate the level of blood circulating POMC prohormone in relation to environmental conditions. *Oecologia (Berlin)* 166:913–921.
- Roulin, A., J. Gasparini, P. Bize, M. Ritschard, and H. Richner. 2008. Melanin-based colorations signal strategies to cope with poor and rich environments. *Behavioral Ecology and Sociobiology* 62:507–519.
- Rowe, L., and Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society B: Biological Sciences* 263:1415–1421.
- Rushton, J. P. 2004. Placing intelligence into an evolutionary framework or how *g* fits into the *r*-*K* matrix of life-history traits including longevity. *Intelligence* 32:321–328.
- Sæther, B. E. 1988. Pattern of covariation between life-history traits of European birds. *Nature* 331:616–617.
- Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79:241–277.
- Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240–243.
- Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–988.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.

- . 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Svanback, R., and D. Schluter. 2012. Niche specialization influences adaptive phenotypic plasticity in the threespine stickleback. *American Naturalist* 180:50–59.
- Van de Pol, M. 2012. Quantifying individual variation in reaction norms: how study design affects the accuracy, precision and power of random regression models. *Methods in Ecology and Evolution* 3:268–280.
- Vercken, E., M. Massot, B. Sinervo, and J. Clobert. 2007. Colour variation and alternative reproductive strategies in female of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* 20:221–232.
- Vercken, E., B. Sinervo, and J. Clobert. 2008. Colour variation in female common lizards: why we should speak of morphs. A reply to Cote et al. *Journal of Evolutionary Biology* 21:1160–1164.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–139.
- Wiersma, P., A. Munoz-Garcia, A. Walker, and J. B. Williams. 2007. Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences of the USA* 104:9340–9345.
- Wolf, M., G. S. van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584.
- Associate Editor: Tony D. Williams
Editor: Judith L. Bronstein



Tawny owls (*Strix aluco*) in Switzerland. *Top*, a free-living adult; photo credit: Guillaume Emaresi. *Bottom*, a chick; photo credit: Pierre-Alain Ravussin.