Experimental evidence that adult antipredator behaviour is heritable and not influenced by behavioural copying in a wild bird

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Knowledge of the relative importance of genetics and behavioural copying is crucial to appraise the evolvability of behavioural consistencies. Yet, genetic and non-genetic factors are often deeply intertwined, and experiments are required to address this issue. We investigated the sources of variation of adult antipredator behaviour in the Alpine swift (Apus melba) by making use of long-term behavioural observations on parents and cross-fostered offspring. By applying an ‘animal model’ approach to observational data, we show that antipredator behaviour of adult Alpine swifts was significantly repeatable over lifetime (r = 0.273) and heritable (h2 = 0.146). Regression models also show that antipredator behaviours differed between colonies and sexes (females were more tame), and varied with the hour and year of capture. By applying a parent–offspring regression approach to 59 offspring that were exchanged as eggs or hatchlings between pairs of nests, we demonstrate that offspring behaved like their biological parents rather than like their foster parents when they were adults themselves. Those findings provide strong evidence that antipredator behaviour of adult Alpine swifts is shaped by genetics and/or pre-hatching maternal effects taking place at conception but not by behavioural copying.

Keywords: Tachymarptis melba; behavioural syndromes; cross-fostering experiment; personality; antipredator behaviour

1. INTRODUCTION

How an individual behaves in different situations is likely to have important fitness consequences [1–5]. Ideally, to maximize its fitness, the same individual should adjust its behaviour to different contexts, for example by behaving aggressively against conspecifics intruding their territory but not against predators. Yet, evidence is accumulating from a wide range of animal species that individuals usually exhibit consistent behavioural differences over time and across situations, thus bringing into question the adaptive value and evolvability of behavioural consistencies, also termed temperament, coping style, personality or behavioural syndrome in the literature [6–13].

To appraise the evolution of behavioural consistencies, one key step is to gather knowledge on the heritability [9,14,15] as selection cannot affect the evolution and maintenance of behavioural consistencies unless they are heritable [16,17]. As total phenotypic variation in temperament among individuals could be owing to genetic, maternal and/or environmental factors, heritability analyses have to estimate their relative contributions. There is compelling evidence for the genetic basis of temperament, provided mostly by studies conducted under laboratory conditions [9,14]. For instance, Dingemanse et al. [18] have recently demonstrated heritable variation in behaviours such as boldness towards predators, explorative behaviour of novel environment or novel conspecifics, sociability and activity levels in the three-spine stickleback (Gasterosteus aculeatus). However, an individual’s temperament is also likely to be affected by the complex interactions of its genes and the timing and type of environmental influences it experiences during its development [18–21]. In particular, maternal effects may play an important role in fine-tuning offspring behavioural responses to their environment [20,21], and can enable rapid adaptive and stable phenotypic changes in temperaments [22]. Accordingly, recent studies have demonstrated that mothers can alter the behaviour of their offspring by transferring hormones to them via eggs in oviparous vertebrates and via placenta and milk in mammals. Even subtle changes in such hormonal transfer can induce long-lasting changes in offspring fearfulness, aggressiveness or risk-taking behaviour [6,21,23,24]. In species with extensive parental care, offspring exposure to the behaviours of the individuals that raise them also has the potential to alter their behavioural phenotypes [25–28]. Such behavioural ‘copying’ has been demonstrated by cross-fostering experiments where offspring behaved more like their foster parents than like their biological parents when they grew up [27,28]. Hence, parental effects can have profound ‘indirect genetic effects’ on offspring behaviour, which can either...
mask or accentuate the contribution of inter-individual additive genetic variance on temperament and, correspondingly, slow down or accelerate the evolution and maintenance of adaptive temperament variation in the wild [15]. Therefore, a crucial step in gaining a comprehensive understanding of the evolvability of temperaments is the assessment of the relative importance of genetics and parental effects on their development.

In the present study, we addressed this question by looking at the origins of antipredator behaviour of wild adult Alpine swifts (Apus melba) while incubating their eggs or brooding their nestlings. As nest predation is an important source of mortality in most animals [29], including swifts [30,31], behaviours affecting its extent are likely to be under strong selection, and should therefore provide a relevant context for assessing the adaptive value of behavioural consistencies. Parents often face the dilemma of staying and defending their offspring against a predator, and in turn placing themselves at risk, or flushing in front of a predator at the risk of losing their reproductive investment [32]. Hence, we scored antipredator behaviour of parents based on how they individually responded to a human intruder at their nest. The behavioural data used were collected over 8 years in two different Alpine swift colonies, following the same individuals and their progeny. All individuals and their offspring remained in their natural environment, only coming into human contact during data collection, minimizing to a great extent the influence of artificial and laboratory settings [7,9]. First, we assessed inter-individual variation in adult antipredator behaviour by fitting mixed regression models to test the influence of sex, colony, year, day and hour of capture on the studied behaviour. Second and after controlling for the significant pre-cited non-additive genetic sources of variation in adult antipredator behaviour, we applied an ‘animal mixed model’ approach to dissect the phenotypic variance of adult antipredator behaviour ($V_\text{p}$) in additive genetic variance ($V_A$), permanent environmental effect ($V_R$) and residual environmental variance components ($V_\text{RE}$ i.e. $V_p = V_A + V_\text{RE} + V_\text{EO}$) [33], thus allowing estimation of repeatability of adult antipredator behaviour (i.e. $r = V_\text{RE}/V_p$) and of heritability in the narrow sense (i.e. $h^2 = V_A/V_p$). Finally, to disentangle the significance of genetics and indirect genetic effects on the variance in antipredator behaviour of adult swifts, we used a cross-fostering experimental design where offspring were swapped between pairs of nests. When the cross-fostered individuals were subsequently recruited in the study population, their adult antipredator behaviour was tested the same way their parents were tested, thus allowing us to examine the resemblance of the offspring temperament with that of their biological and foster parents. In addition, because offspring were cross-fostered as either eggs or hatchlings, variance in offspring temperament associated with the biological parents can be caused by genetic factors and/or pre-hatching parental effects, and variance in offspring temperament associated with its foster parents can be caused by post-hatching parental effects and/or environmental effects. Hence, we predicted that, if genetics and/or pre-hatching parental effects explain significant variation in offspring temperament, the offspring should behave like their biological parents rather like their foster parents when they are adults themselves. In contrast, the opposite would be observed if post-hatching parental effects and/or environmental factors account for variation in offspring temperament. To our knowledge, this is the first experimental study aiming to disentangle additive genetic effects from indirect genetic (i.e. parental) effects on behavioural consistencies using free-living subjects in the wild.

## 2. MATERIAL AND METHODS

(a) The Alpine swift

The Alpine swift is a migrant colonial apodiform bird that breeds in holes of cliffs and under the roof of tall buildings. It feeds on insects caught exclusively in flight. It is socially monogamous and reproduces in colonies counting up to several hundred breeding pairs. A single clutch is produced per year with one to four eggs being laid at 1-day intervals (mean ± s.e. clutch size: 2.65 ± 0.02, $n = 1506$ clutches). Hatching is synchronous, with eggs issued from the same clutch hatching usually within a 24 h interval [30]. Males and females have equal investment in the brood. Both parents incubate the eggs for 20 days and feed the offspring up to fledging taking place at 50–69 days after hatching (hatching day is defined as day 0) [34]. Adults are sexually mature at the age of 2 or 3 years and the oldest recaptured bird reported was 26 years old (Swiss Ornithological Station, 2010, personal communication). Natal and breeding dispersal are limited with most birds breeding in the colony where they were born [34].

(b) General procedure

The fieldwork was conducted over 11 breeding seasons between 2000 and 2010 in two Swiss colonies located in clock towers in Bienne (ca 100 breeding pairs; 47° 10’ N, 7° 12’ E) and Solothurn (ca 50 breeding pairs; 47° 12’ N, 7° 32’ E). The two cities have a distance of 21 km between each other. Each year nests were regularly visited to determine laying date, clutch size and brood size at hatching and fledging. Because we visited colonies every day during the hatching period, we could determine hatching date of all nestlings which were individually marked with a non-toxic permanent colour mark before being ringed at 10 days with an aluminium numbered band. Each year, adults were captured while sitting on their eggs or hatchlings, and either a drop of blood or feathers were collected from each adult to determine sex from genomic DNA using molecular techniques [35].

(c) Behavioural scoring

Antipredator behaviour was estimated by the same observer (P.B.) in the form of discrete behavioural scores ranging from 0 to 2 given based on how each breeding adult behaved towards the ‘human intruder’ during approach and capture. We assigned the score 0 to individuals that flushed from the nest upon first audio and/or visual detection of capturer, 0.5 to individuals that remained on the nest during capturer approach but flushed upon extension of capturer’s hand to grab the individual, 1 to individuals that remained immobile on the nest during approach and capture, 1.5 to individuals that remained immobile on the nest during capturer approach but started to move towards the capturer’s hand, to flap their wings and to grasp at any approaching object (i.e. hand) with their claws (defined hereafter as ‘aggressive behaviour’), 2 to individuals that behaved aggressively upon...
the capturer’s approach and during capture. Because breeders access their nests via small holes under the roof, and the mean distance between nests and colony entrances ± s.e. is 94 ± 1.7 cm, flushing adults were caught before leaving the building to record their identity. We collected 2308 behavioural observations from 620 individuals between 2003 and 2010. Note that although we divided the variation in antipredator behaviour of adult Alpine swifts into five discrete categories (i.e. 0, 0.5, 1.0, 1.5, 2), the natural variation of this behaviour is most likely continuous, as denoted by the large inter- and intra-individual variance in behavioural scores attributed to the same individuals captured one time or more (figure 1). Thus, hereafter we assumed our behaviour scoring to be univariate and continuous.

**Figure 1.** Intra- and inter-individual variation in antipredator behaviour in free-living adult Alpine swifts. Birds are ranked from left to right based on their mean behavioural response; individuals that generally flush at human approach (score of 0) are depicted by markers on the leftmost side of the graph, and correspondingly individuals that generally behave aggressively towards the intruder (score of 2) are presented on the rightmost side. The size of circles is proportional to the number of observations per individual for a given behaviour score (horizontal, inter-individual variation), and individuals can be represented by several circles if they showed behavioural variation among observations (vertical, intra-individual variation).

**Notes:**

- The graph shows the variation in antipredator behaviour of adult Alpine swifts, with birds ranked from left to right based on their mean behavioural response. Individuals scoring 0 generally flush at human approach, while those scoring 2 behave aggressively towards the intruder.
- The size of circles is proportional to the number of observations per individual for a given behaviour score.
- Individuals can be represented by several circles if they showed variation among observations.

**Cross-fostering experiments**

To experimentally investigate whether antipredator behaviour of adult Alpine swifts has a genetic background or is the outcome of behavioural copying from the individuals that raised them, we carried out cross-fostering experiments between 2002 and 2006 in Solothurn and between 2000 and 2008 in Bienne. We either cross-fostered the complete clutches or only 1 or 2 two-day-old hatchlings, while their siblings remained in the nest of origin (so-called full cross-fostering experiment; n = 74 and 76 nests in Bienne and Solothurn, respectively) or only 1 or 2 two-day-old hatchlings, while their siblings remained in the nest of origin (so-called partial cross-fostering experiment; n = 150 and 74 nests in Bienne and Solothurn, respectively; see also study of Bize et al. [34] for additional information on nest sample sizes and experimental procedures). All the experimental nests were from first (i.e. non-replacement) clutches. Cross-fostered nestlings were raised by their foster parents until fledging.

**Statistical analyses**

We applied a three-step approach to investigate the contribution of additive genetic variance and behavioural copying on antipredator behaviour of adult Alpine swifts, namely: (i) the use of mixed regression models to explore the importance of non-genetic variation on individual variation in antipredator behaviour, (ii) the use of animal mixed models to estimate the repeatability and heritability for antipredator behaviour, and (iii) the use of parent–offspring regression models to test for the occurrence of behavioural copying.

**Mixed regression models**

To explore the importance of the colony, sex, year, day, and hour of capture on variation in adult risk-behaviour, we fitted a mixed regression model [36] with the behavioural score of each individual at each capture as dependent variable, with the previously mentioned terms as fixed explanatory variables, and with the individual identity as random explanatory variable. In the starting regression model, we also fitted quadratic terms for year, day and hour of capture to accommodate for possible nonlinear changes in risk taking behaviour over years, days and hours, respectively. Individual identity was entered as a random term in the model as there were multiple measurements of most individuals (n = 2308 behavioural observations from 620 individuals). Because antipredator behaviour might also vary with individual age, we ran additional analyses including age as a covariate in the starting model previously described but restricting the dataset to birds of known age only (n = 1712 behavioural observations from 446 individuals). To compare competing models and choose the one that best describes the observed variation in antipredator behaviour, we used Akaike’s information criteria (AIC) [37]. Non-significant fixed effects were removed one after another from the initial full model, starting with the least significant second-order terms, until finding the model with the lowest AIC score. Note that we based our calculations on maximum likelihood to compare the fit of our mixed models and on restricted maximum likelihood to...
approximate the value of the parameters retained in the best model [36].

(ii) Animal mixed models

The 'Animal Model' approach allows separating phenotypes into fixed and random effect variance components by comparing the phenotypes of all known relatives in a pedigree across generations [33,38]. We used a pedigree (n = 5873 individuals) based on observed pairing rather than genetic parentage, and in cases where eggs or chicks had been moved between nests, we always assigned the biological parents rather than the foster parents. It follows that offspring reared by parents who had themselves been cross-fostered where assigned to their biological parents and grandparents rather than their foster parents and grandparents, thus tracking down genetic inheritance through our pedigree. We fitted as fixed effect the variables previously identified as significant by our mixed regression model approach, and we included as random effect the pedigree information and individual identity which allowed us to estimate additive genetic variance (V_A) and permanent environment effects (V_PE), respectively. V_PE takes into consideration repeated behavioural records on individuals throughout their lifetimes, and thus it accounts for and estimates the variance caused by persistent differences between individuals that are not already attributed to additive genetic variance [33]. Therefore, our animal model allowed us to partition total phenotypic variance (V_p) in V_p = V_h + V_PE + V_R, where V_R is the residual variance, and to compute repeatability as r = V_PE/V_p and heritability in the narrow sense as h^2 = V_A/V_p. The pruned pedigree associated with our animal model (i.e. the pedigree restricted to individuals with known behavioural scores and accounting for a pedigree link) contained 788 individuals, went back at most three generations, and contained 207, 345 and 384 links between full sibs, maternal sibs and paternal sibs, respectively. Maternal sibs are offspring born from the same mothers mating with different males in different years, and vice versa for paternal sibs. Although the animal model can allow accounting for and estimating the variance owing to common mother environment and/or common father environment by including in the model individual identity of the mother and/or of the father as random effects [33], our pedigree was unfortunately not large enough to allow such detailed level of variance partitioning. Indeed, the pruned pedigree restricted to individuals with known behavioural scores, known behavioural scores of their rearing parents and accounting for a pedigree link was reduced to 384 individuals, with 61, 96 and 112 links between full sibs, maternal sibs and paternal sibs, respectively.

(iii) Parent–offspring regression models

To accommodate for the low number of subjects with known individual behavioural scores and known behavioural scores of their biological and rearing parents, we used the classical 'parent–offspring regression' approach [17]. We restricted our analysis to 59 subjects that meet the three following criteria: (i) they had been exchanged between nests as egg (n = 24) or as hatching (n = 35); (ii) they returned to breed in Bienne (n = 32) or Solothurn (n = 27), and in turn their adult antipredator behaviour had been scored; (iii) the antipredator behaviour score of their two biological parents and their two foster parents had been scored; and (iv) they were born from parents that have not been cross-fostered themselves. We tested whether antipredator behaviour in adulthood of Alpine swifts has a genetic background, or is the outcome of behavioural copying from the individuals that raised them using a multivariate regression model with offspring behavioural score as response variable and with biological midparent behavioural scores and foster midparent behavioural scores as explanatory covariables. To investigate whether the timing of cross-fostering (egg versus hatchlings) had a consequence on the development of offspring behaviour, we entered the cross-fostering stage as a third explanatory variable. A significant relationship between the behaviours of offspring and their biological parents would provide evidence for additive genetic variance, while a significant association between the behaviours of offspring and their foster parents would provide evidence for behavioural copying. We calculated heritability in the narrow sense (h^2) as the slope of the relationship between offspring and their biological parents after accounting for the relative contribution of foster parents [17].

Regression models were performed using the R package lme and animal models using the ASReml-R software [39]. For all our models, we used a Gaussian error structure and we visually checked for normality of the distribution of the residuals using quantile–quantile plots. We assessed the statistical significance of fixed effects and random effects of our mixed models using F-statistics and log-likelihood tests, respectively. Information on pruned pedigrees was calculated with the R package Pedantics [40]. Mean values are reported as ± 1 s.e.

3. RESULTS

Mixed regression analyses showed that the antipredator behaviour at human approach of adult Alpine swifts while incubating their eggs or brooding their chicks was significantly influenced by the sex, colony, year of capture and hour of capture, but not by the day of capture (table 1a). Males were more prone to flush in response to human approaches than females, and individuals in Bienne were more prone to flush than those in Solothurn (figure 2a). Levels of adult antipredator behavioural responses declined significantly from 2003 to 2010, with most of the decline occurring between 2003 and 2004 (figure 2b). Antipredator behaviour also varied over the course of the day, with a significant effect of squared hour of the day indicating that individuals were more prone to flush from their nest in the morning or in the evening than around midday (table 1a and figure 2c). Additional analyses restricted to known-age birds provided no evidence that antipredator behaviour varied with age (table 1b).

After controlling for the variance explained by the fixed factors highlighted in table 1a, animal mixed models show significant levels of permanent environment effects (V_PE = 0.071 ± 0.017, z = 4.19, p < 0.0001) and additive genetic variance (V_A = 0.038 ± 0.017, z = 2.20, p = 0.032) on adult antipredator behaviour (figure 3), which in turn translated into a significant behavioural repeatability of 0.275 and heritability of 0.146. For comparison, variance components without conditioning for the variance explained by fixed effects were of V_PE = 0.070 ± 0.018 (z = 3.83, p < 0.0001) and V_A = 0.057 ± 0.019 (z = 2.93, p = 0.004), which in turn translated into a behavioural repeatability of 0.251 and heritability of 0.205.
Table 1. Final results of the mixed models analysing the variation in antipredator behavioural score in free-living adult Alpine swifts. Results of model (a) are based on the full dataset; the full model included colony (Solothurn versus Bienne), year and year$^2$ of capture, day and day$^2$ of capture, and hour and hour$^2$ of capture as fixed effects, and individual identity (i.e. the ring number) as a random factor to take into account the non-independence of multiple behavioural observations from the same individuals. Results of model (b) are based on a dataset restricted to individuals of known age; thus, age was entered as an additional fixed effect in the full model of (a). Competing models were compared using Akaike information criterion (AIC), and the final models are the ones with the lowest AIC value.

(a) full dataset: 2308 observations from 620 individuals
fixed effects terms estimate s.e. d.f. $F$ $p$-value
intercept 17 306.7 8416.3 0.004 1,1261 2.3 0.133
sex (M) −0.069 0.033 1,1684 41.2 <0.001
colony (Solothurn) −0.223 0.035 1,1684 9.7 0.002
year −17.239 8.390 1,1684 17.220 9.534 1,1261 6.9 0.009
year$^2$ 0.004 0.002 1,1684 2.8 0.092
hour 0.139 0.035 1,1684 3.3 0.070
hour$^2$ −0.005 0.001 1,1684 15.6 <0.001
random effects terms variance components 95% CI
ring 0.328 (0.301; 0.357)
error 0.387 (0.374; 0.400)

(b) dataset restricted to birds of known-age: 1712 observations from 446 individuals
fixed effects terms estimate s.e. d.f. $F$ $p$-value
intercept 17 286.7 9564.3 0.005 1,742 2.99 <0.004
age −0.003 0.002 1,742 1.7 0.194
sex (M) −0.057 0.037 1,742 2.4 0.123
colony (Solothurn) −0.231 0.040 1,742 33.8 <0.001
year −17.220 9.534 1,742 11.261 6.9 0.009
year$^2$ 0.004 0.002 1,742 2.3 0.133
hour 0.171 0.039 1,742 2.6 0.110
hour$^2$ −0.006 0.001 1,742 19.5 <0.001
random effects terms variance components 95% CI
ring 0.310 (0.281; 0.343)
error 0.377 (0.363; 0.392)

Parent–offspring regressions show that the antipredator behaviour of cross-fostered offspring was significantly related with the antipredator behaviour of biological parents (slope ± s.e.: 0.326 ± 0.109; $t_{56} = 2.99$, $p = 0.0042$; figure 4) but not with that of foster parents (slope ± s.e.: $-0.016 ± 0.119$; $t_{53} = -0.13$, $p = 0.85$; figure 4). The cross-fostering stage had no significant effect when entered alone in the model ($t_{53} = 0.31$, $p = 0.76$) or in interaction with genetic midparent behavioural score ($t_{53} = -0.75$, $p = 0.45$) or foster midparent behavioural score ($t_{53} = -0.28$, $p = 0.78$). The cross-fostering stage was therefore removed from the final regression analysis presented above. Adults mate assortatively based on their antipredator behaviour score (estimate ± s.e. = 0.11 ± 0.03, $F_{1,742} = 12.61$, $p = 0.004$; after controlling for the effect of year and colony), and thus we did not investigate separately the maternal and paternal contributions to variation in offspring antipredator behaviour.

4. DISCUSSION
Variation in temperament among individuals can be due to genetic, parental and/or environmental factors, and quantitative genetic analyses aim to partition the relative contributions of genetic versus non-genetic factors to the total phenotypic variance in a population [17]. Because genetic and non-genetic factors are often intermingled, experiments are required to address this question. Here, we report results from a cross-fostering experiment assessing the relative importance of genetics and behavioural copying on behavioural consistencies in antipredator behaviour of free-living Alpine swifts. Although we measured antipredator behaviour of adults based on how they individually responded to a human intruder at their nest rather than to a natural predator, this test is likely to match situations occurring in the wild where parents facing disturbance at the nest have to quickly decide between either flushing, and thereby risking losing their current reproductive investment, or by staying and defending their nest at the risk of being predated [32]. By exchanging eggs or hatchlings between pairs of nests, we demonstrate that offspring had similar antipredator behaviour to their biological parents, but not to their foster parents, when they were adult themselves. Thus, despite Alpine swift nestlings staying on average 56 days in the nest [41], which offers a long period for foster parents to influence the behaviour of their foster offspring, our cross-fostering experiment...
provides no evidence for the occurrence of post-hatching parental effect on adult antipredator behaviour in this long-lived bird species. We also found that the stage (egg versus hatchling) at which offspring were cross-fostered between pairs of nests did not contribute to variance in offspring temperament, which allows us to rule out the effect of parents during incubation and/or briefly after hatching or later in the post-hatching period on the development of offspring temperament. Hence, our results indicate that antipredator behaviour of adult Alpine swifts is determined by genetic factors and/or maternal (or paternal) effects taking place at conception. Indeed, there is growing evidence in bird species that mothers can modulate the behaviour of their offspring by transferring hormones to them via the egg yolk [42], with hormones such as noradrenaline, testosterone and corticosterone being associated with changes in antipredator behaviour [6,23]. Hence, to further tease apart genetic and maternal hormone transfer effect on the evol-

vability of offspring temperament, more studies are required on the variation in maternal hormone transfer [43] and on the consequences of maternal hormones on offspring behaviour [44].

Measurements of antipredator behaviour of the same individual repeated over several trials show that this behaviour was consistent over time, with a repeatability estimate of 0.27. This is slightly lower than the average repeatability value of 0.37 (95% CI: 0.35–0.38) across all behavioural categories and all taxa recently reported by Bell et al. [45] in their meta-analysis. However, repeatability estimates are known to decline with increasing time interval between two successive measurements, and most repeatability esti-

mates included in the meta-analysis by Bell et al. were based on repeated measurements of the same individuals within a few hours or days [45]. In this study, antipredator behaviour of the same individuals was usually measured at 1 year intervals and during up to 8 consecutive years, thus demonstrating that the studied behaviour was consistent over a substantial part of the lifespan of Alpine swifts. Accordingly, there was also no evidence that antipredator behaviour responses changed with the day of capture (a good surrogate of the number of nest disturbance within each season) and age, and in turn no evidence that adult swifts show habituation to human intrusion to their nest. Yet, the finding that antipredator behaviour was influenced by the hour of capture indicates nonetheless that individuals had not completely fixed behavioural response but displayed some behavioural plasticity [10]. Evidence for behavioural consistency over long timescales remains none-

theless rare [46,47], presumably owing to the difficulty of
following the same individuals over long periods [11], and is a challenging evolutionary phenomenon as long-term behavioural consistencies may lead to suboptimal behaviour when behavioural carryovers occur across situations that favour alternative behavioural responses [11,48].

Repeatability establishes the ceiling value to the heritability [17], and the obtained repeatability estimate of 0.27 suggests at most a moderate field heritability of antipredator behaviour in adult Alpine swifts. Accordingly, our animal model approach yielded a significant heritability estimate of 0.15 and biological parent–offspring regression gave a significant heritability estimate of 0.33. The lower heritability estimate of the animal model compared with the parent–offspring regression was an expected result; the inclusion of individual replicates to the animal model increases the sampling accuracy, expected result; the inclusion of individual replicates to the animal model increases the sampling accuracy, and changes over time support the idea that adult antipredator behaviour is under selection and, by extension, that genetic midparent antipredator behavioural score in wild-derived great tits (Parus major) [50] and of 0.21–0.89 obtained from a breeding experiment on adult antipredator behaviours in wild-derived dumpling squids [2]. Altogether, those different approaches support the idea that the heritability of adult risk-taking behaviour in wild animals is low to moderate, which might arise if such behaviour is under strong natural selection, thereby leading to a depletion of additive genetic variation in natural populations [50].

Interestingly, we found that males were more prone to flush than females, individuals in the Solothurn colony were more prone to flush than those in the Bienne colony, and that antipredator behaviour at the population level declined during the studied period. Such differences and changes over time support the idea that adult antipredator behaviour is under selection and, by extension, that this temperament is heritable and evolves in response to intrinsic or extrinsic factors such as sex-specific requirements or local breeding environment. Theoretical models suggest that sexual differences in nest defence behaviour are expected whenever there is a difference in confidence of parenthood, ability to raise offspring unaided, ability to re-nest or life-history strategy [51,52]. Paternity analyses have not yet been carried out in the Alpine swift, but in a related colonial species (the common swift, Apus apus) extra-pair paternity is rare. Martins et al. [53] found only four chicks (4.5%) out of 88 were extra-pair. In the socially monogamous Alpine swift, parental care is shared and one parent is unable to raise offspring unaided [41]; P.B., 1999–2011, personal observation). Re-nesting is also very rare (i.e. less than 2% of the breeding attempts; P.B., 1999–2011, personal observation). Hence, variation in either confidence of parenthood, ability to raise offspring unaided or ability to re-nest is unlikely to drive the difference in temperament observed between male and female swifts. In contrast, a recent study has pointed out that male and female swifts might have different life-history strategies, with female fitness being sensitive to fecundity and male fitness to survival [54]. It suggests that the greater sensitivity to disturbance at the nest of males compared with females might be driven by greater survival benefits in males. Sensitivity to disturbances can also evolve in relation to nest density and location, and in turn competition for nesting site or risk of nest predation [55]. Because of their colonial habits and frequent nest re-use from year to year [41,56,57], swifts are thought to enter into competition for nesting sites [58,59]. The two main differences between the colonies at Bienne and Solothurn are that there are about two times more breeding pairs in Bienne, and that corvids (which are potential nest predators) use the same breeding site in Bienne. Hence, one hypothesis is that greater local competition for nesting sites favours the recruitment in Bienne of individuals with a lower sensitivity to disturbances. Selective factors driving the decline in antipredator behaviour at the population level over the study period remain unclear and deserve further study. To provide insights on the evolution and maintenance of inter-individual variance of antipredator behaviour, work is now required on the link between temperament and fitness in male and female adult Alpine swifts reproducing under various environmental factors. Although evidence is accumulating that variation in temperament can have strong fitness consequences [1–5], it is poorly understood whether selection on individual temperament is sex specific [60].

Figure 4. Relationship between antipredator behavioural score of cross-fostered offspring and (a) biological midparents and (b) foster midparents in free-living adult Alpine swifts. For illustrative purpose, a regression line of slope 1 and intercept 0 is shown in both (a,b) representing the theoretical heritability of 1.

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