Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion

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SUMMARY

Since most bird species are socially monogamous, variation among species in social mating systems is determined largely by variation in the frequency of mate desertion. Mate desertion is expected to occur when the benefits, in terms of additional reproductive opportunities, outweigh the costs, in terms of reduced reproductive success from the present brood. However, despite much research, the relative importance of costs and benefits in explaining mating system variation is not well understood. Here, we investigate this problem using a comparative method. We analyse changes in the frequency of mate desertion at different phylogenetic levels. Differences between orders and families in the frequency of desertion are negatively associated with changes in the potential costs of desertion, but are not associated with changes in the potential benefits of desertion. Conversely, differences among genera and species in the frequency of desertion are positively associated with increases in the potential benefits of desertion, but not with changes in the potential costs of desertion. Hence, we suggest that mate desertion in birds originates through a combination of evolutionary predisposition and ecological facilitation. In particular, ancient changes in life-history strategy determine the costs of desertion and predispose certain lineages to polygamy, while contemporary changes in the distribution of resources determine the benefits of desertion and thereby the likelihood that polygamy will be viable within these lineages. Thus, monogamy can arise via two very different evolutionary pathways. Groups such as albatrosses (Procellariidae) are constrained to social monogamy by the high cost to desertion, irrespective of the potential benefits. However, in groups such as the accentors (Prunellidae), which are predisposed to desertion, monogamy occurs only when the benefits of desertion are very limited. These conclusions emphasise the additional power which a hierarchical approach contributes to the modern comparative method.

1. INTRODUCTION

In most birds, one male and one female form a pair and raise a brood together, and they are conventionally termed monogamous, even if paired for only one brood... The main advantage of monogamy is that, where the sex ratio is not badly distorted, both male and female leave, on average, most offspring if both help to raise a brood... The three alternatives to monogamy ['polygyny', 'promiscuity' and 'polyandry'] are sometimes grouped as 'polygamy'... The ecological factors making these abnormal types of pairing more advantageous than monogamy are not clear. They are least uncommon in nidifugous species which do not feed their young and in vegetarian nidicolous birds, probably because in such species one parent can raise the family unaided.

David Lack (1968), pp. 4–5

Most explanations of variation in social mating systems among bird species derive from David Lack's insights that (i) most birds are socially monogamous,

(ii) they are socially monogamous because mate desertion reduces the probability of successfully rearing a brood, and (iii) differences between species in the frequency of desertion are a function of the probability that a single parent can raise a brood. These explanations, therefore, emphasize the importance of differences between species in the costs associated with desertion (i.e. reduced reproductive success from the present brood); differences between species in the benefits of desertion (i.e. additional reproductive opportunities) are considered to be of minor importance. Under such explanations it is easy to appreciate why groups with extremely long periods of parental care, such as albatrosses (Procellariidae), are typically monogamous whereas groups with little parental care, such as pheasants and grouse (Phasianidae), are typically polygamous (see Sillén-Tullberg & Temrin (1994), Temrin & Sillén-Tullberg (1994, 1995), for a quantitative demonstration of this view).

Explanations of the type summarized above, have been recently challenged using two lines of evidence.

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First, it is not established that differences in the frequency of mate desertion (and polygamy) are in fact associated with differences in the cost of desertion. For example, Webster (1991) showed that the direct costs of desertion, in terms of reduced fledging success, were no lower in frequently polygamous passerines than in monogamous passerines. Second, the incidence of mate desertion (and polygamy) can be altered within species without manipulating the costs of desertion. For instance, both Smith *et al.* (1982) and Hannon (1984) have shown that mate desertion can be induced in otherwise socially monogamous species by experimentally increasing the availability of mates. Observations of these kinds are contrary to the assumptions of the traditional, costs-driven view of avian mating system variation and suggest that variation in the potential benefits of desertion may be more important than has been commonly assumed (see Emlen & Oring 1977).

The aims of this paper are to use modern comparative techniques to (i) identify when, in evolutionary time, the observed variation between species in the frequency, costs and benefits of mate desertion originated, and (ii) discover whether changes in the frequency of desertion are correlated with changes in the costs and/or benefits of desertion. Hence, we characterize variation in social mating systems by measuring the frequency of mate desertion and thereby assume that, in birds, differences between species in the frequency of mate desertion are primary in determining differences in social mating systems. This assumption is based, first, on our definition of social monogamy as being the state where one male and one female remain together and cooperate in breeding for the duration of at least one breeding attempt (see Wickler & Seibt 1982; Gowaty 1985; Gowaty 1996), and second, on the observation that polygamy is a derived state in most avian clades (see McKittrick 1992; Sillén-Tullberg & Temrin 1994; Temrin & Sillén-Tullberg 1994, 1995; Wesolowski 1994). Our analyses are, therefore, designed to identify ecological differences between socially monogamous and socially polygamous species, but cannot differentiate between different forms of polygamy. Further work is required to identify the ecological differences that lead, for instance, to polyandry rather than polygyny, lekking rather than harem defence, and cooperative rather than non-cooperative polyandry.

2. METHODS

We collated published and unpublished data concerning wild populations of 202 bird species. These data yielded species-typical estimates of the frequency of mate desertion, two indices of the potential cost of mate desertion (direct fecundity-cost, and duration of chick-feeding) and two indices of the potential benefit of mate desertion (extent of nest-aggregation, and food-aggregation). This database is available from the authors on request.

The frequency of mate desertion was ranked as follows: 0, desertion not recorded; 1, desertion in < 5% of broods; 2, desertion in > 5% but < 50% of broods; 3, desertion in > 50% of broods. In our database, 124 (61%), 31 (15%), 21 (10%) and 26 (13%) species were assigned to each of these

categories, respectively. We did not include species exhibiting no parental care such as brood-parasites and the megapodes.

Our first index of the costs of desertion was the direct fecundity-cost of desertion which was measured as the difference in fledging success between uniparental broods and biparental broods: $[1 - (\text{the mean number of independent young produced by uniparental care} / \text{mean number of uniparental young produced by biparental care})]$ (Wolf *et al.* 1988; Bart & Tornes 1989; Webster 1991; Gowaty 1996). For this variable we could only find data for 59 of the 202 species and all analyses including this variable were limited to these species. Due to this extreme shortage of data, we were not able to look at the possibly confounding effects of variation between studies in the phase in the breeding cycle at which the desertion occurred (laying, incubation, or hatching), the manner in which the desertion occurred (experimental manipulation or natural death of one partner), and the form of the biparental comparison (sham manipulation or natural biparental care) (see Gowaty (1996) for discussion). Hence, this variable should be viewed as a relatively crude index of the true fecundity costs of desertion.

Our second index of the cost of desertion was the duration of the chick-feeding period, measured in days. This index is based on evidence, from both experimental and comparative studies, that parents which are either fully or partially deserted by their partner, and therefore provide uniparental care for their offspring, suffer a higher rate of mortality than do those parents which are not deserted by their partner (Clutton-Brock 1991; Owens & Bennett 1994). Here, we assume that the severity of this mortality cost of mate desertion is positively related to the duration of chick feeding. Again however, this is likely to be a crude measure of the costs of desertion since its accuracy relies on the secondary assumption that an increase in the rate of mortality experienced by the deserted parent will reduce the fitness of the deserting parent.

Our two indices of the benefits of desertion are the degree of nest-aggregation and the degree of food-aggregation. These indices are based on the assumption that the availability of additional mates can be estimated by measuring the extent to which resources are aggregated, and thereby defensible by members of one sex in order to monopolize matings with the opposite sex (Wittenberger 1976; Emlen & Oring 1977). The extent of nest-aggregation was measured as nests per hectare. Where more than one measure of nesting density was found in the literature, the highest value was used. The extent of food-aggregation was measured on a four-point scale: 0, foraging areas of adjacent nests do not abut; 1, foraging areas of adjacent nests abut but do not overlap; 2, foraging areas of adjacent nests overlap < 50%; 3, foraging areas of adjacent nests overlap > 50%. Once again though, these indices can only be regarded as rough estimates of the availability of additional mates.

Because closely related species may be more similar to one another than would be expected by chance, the species-typical data were not treated as statistically independent data points. In order to identify and calculate evolutionarily independent data points we used Felsenstein's (1985) independent comparisons method. Specifically, we used the second version of the Comparative Analysis by Independent Contrasts (CAIC) program (Purvis & Rambaut 1995) to employ Pagel's version of the independent comparisons method (Harvey & Pagel 1991; Pagel 1992). Thus, all analyses are based on contrast scores resulting from the CAIC program rather than from species-specific data.

To establish that our results were not dependent on the phylogeny used, we performed each analysis twice, once using the full Sibley and Ahlquist (1990) tapestry phylogeny (branch lengths above the family level based on ΔT_{50H}

values resulting from DNA–DNA hybridization experiments, branch lengths between genera and between species set at 1 unit), and once using a phylogeny based on Cracraft's (1981) morphological taxonomy (all branch lengths set to equal length) (see Owens & Bennett 1994, 1995; Bennett & Owens 1997).

To satisfy our first aim, we wanted to know when, in evolutionary time, the observed variation in the different traits originated. We addressed this question by comparing the amount of variation in a trait at different phylogenetic levels (see Owens & Bennett 1995). We used the CAIC program to calculate the amount of change that occurred in a trait at each phylogenetic branching point, or 'node'. These changes are referred to as 'contrasts'. Unfortunately, the contrasts produced by the CAIC program cannot be used to compare the amount of change that occurred at different phylogenetic levels because these contrasts have been 'standardized' to control for inequalities in the variance expected across phylogenetic levels. The absolute values of these standardized contrasts were, therefore, unstandardized by being multiplied by the square root of the expected variance of the contrast to yield 'unstandardized contrasts'. Then, for each trait, we grouped the unstandardized contrasts according to the phylogenetic level which they represented. For diagrammatic purposes we used four levels of phylogenetic grouping: contrasts between orders; contrasts between families within orders; contrasts between genera within families; and contrasts between species within genera. We also used ANOVAs to test whether unstandardized contrasts were equally distributed, according to size, among phylogenetic levels. In the ANOVA tests only two groupings were used: higher phylogenetic levels (contrasts between orders and between families within orders) and lower phylogenetic levels (contrasts between genera within families and between species within families). This procedure was repeated for each trait in turn.

With respect to our second aim, we wanted to know whether changes in the frequency of desertion are correlated with changes in the costs and/or benefits of desertion. Here, we used the CAIC program to identify the nodes at which evolutionarily independent changes in the index of the frequency of mate desertion occurred, to measure the size of the standardized contrast in the frequency of mate desertion at each of these nodes, and to calculate the relative size and direction of the standardized contrasts in the indices of the costs and benefits of desertion at each of these nodes. We used single linear regression models to test whether there was a relationship between the size and direction of standardized contrasts in the frequency of desertion and the size and direction of standardized contrasts in the indices of the costs and benefits of desertion. We treated our four-point index of the frequency of mate desertion as the dependent variable and sought to explain variation in this variable using the four independent variables; fecundity-cost of desertion, duration of chick-feeding, extent of nest-aggregation and extent of food-aggregation (see Conover & Iman (1981) for rationale for the use of ranked data in linear models). However, because the four-point index of the frequency of mate desertion is a conservative measure of the frequency of desertion, many zero-contrasts were generated for this variable which made the use of parametric statistical methods invalid. We therefore excluded these zero-contrasts from our regression analyses. However, in order to ensure that the exclusion of zero-contrasts did not qualitatively influence the results we repeated all analyses twice using, first, a nonparametric method based on the full set of contrasts, and second, *t*-tests based on the full set of contrasts generated using a comparative method, which assumed that the index of the frequency of mate desertion was a categorical variable

(BRUNCH; Purvis & Rambaut 1995). These additional analyses showed that the exclusion of zero-contrasts did not qualitatively affect the results. Nevertheless, it should be borne in mind that the generation of such a large number of zero-contrasts for the frequency of mate desertion, but not for the other variables, does suggest that there have been a lot of changes in the costs and benefits of desertion that have not translated into substantial changes in the frequency of desertion.

Finally, for all the regression models we investigated whether any associations found were equally pronounced and in the same direction at all phylogenetic levels (see Owens & Bennett 1995; Bennett & Owens 1997). To do so we performed all analyses twice, once with only those contrasts derived from comparisons between recent lineages (between species within a genus or between genera within a family), and once among only those contrasts derived from comparisons between ancient lineages (between families within an order or between orders within the class). All regression models were forced through the origin (Pagel 1992; Purvis & Rambaut 1995).

3. RESULTS

(a) Variation across phylogenetic levels

The different types of trait showed different patterns of variation with respect to phylogenetic level (figure 1). The two indices of the potential costs of desertion were more varied among ancient lineages than among more recent lineages (figure 1*a–d*). For example, when we used the molecular phylogeny to calculate contrasts we found that there was significantly more variation in the duration of the chick-feeding period among higher phylogenetic levels than among lower phylogenetic levels (69% among higher levels, $F_{1,95} = 9.0$, $p < 0.01$). Similarly, when we used the morphological phylogeny we found that there was significantly more variation at the higher phylogenetic levels than at the lower levels in both the duration of chick feeding (72% among higher levels, $F_{1,94} = 13.8$, $p < 0.001$) and the direct fecundity-cost of desertion (91% among higher levels $F_{1,33} = 3.61$, $p < 0.05$). When we used the molecular phylogeny to examine the pattern of variation in the direct fecundity-cost of desertion we found that there was more variation at higher phylogenetic levels compared to lower levels, but that this difference was not significant (79% among higher levels, $F_{1,30} = 1.18$, $p > 0.10$).

The two indices of the potential benefits of desertion tended to vary consistently across all levels (figure 1*e–h*). Hence, there was no significant difference between the amount of variation present at the higher phylogenetic levels and that present at the lower levels. For example, when we used the molecular phylogeny we found that 57% of the variation in nest-aggregation, and 48% of the variation in food-aggregation, was distributed among the higher phylogenetic levels ($F_{1,95} = 0.7$, $p > 0.40$, and $F_{1,95} = 0.0005$, $p > 0.99$, respectively). Similarly, when we used the morphological phylogeny we found that 45% of the variation in food-aggregation occurred among the higher taxonomic levels ($F_{1,94} = 0.61$, $p > 0.40$). The only exception occurred when we used the morphological phylogeny to look at variation in nest-

Figure 1. Variation in the costs, benefits and frequency of mate desertion across four different phylogenetic levels, controlling for phylogeny; (a) variation in direct fecundity-cost of desertion using the molecular phylogeny, (b) variation in direct fecundity-cost of desertion using the morphological phylogeny, (c) variation in duration of period of chick-feeding using the molecular phylogeny, (d) variation in duration of period of chick-feeding using the

Table 1. *Associations between changes in the frequency of mate desertion and changes in the cost and benefits of desertion among ancient lineages, controlling for phylogeny*

(Regression models based on standardized independent contrast scores. All analyses performed on contrasts between ancient lineages only (between families or higher according to the relevant phylogeny). Two independent phylogenies are used. All regressions are single least squares models forced through the origin. Frequency of mate desertion is the dependent variable in all models.)

independent variable	<i>N</i>	<i>r</i>	<i>p</i>	slope ($\pm$ s.e.)
(a) analyses based on molecular phylogeny				
direct fecundity-cost	18	0.78	< 0.001	-0.32 ($\pm$ 0.06)
duration of chick-feeding period	35	0.36	< 0.05	-7.25 ($\pm$ 3.25)
extent of nest-aggregation	35	0.32	> 0.10	
extent of food-aggregation	35	0.10	> 0.50	
(b) analyses based on morphological phylogeny				
direct fecundity-cost	19	0.86	< 0.001	-0.34 ($\pm$ 0.05)
duration of chick-feeding period	33	0.41	< 0.05	-8.68 ($\pm$ 3.43)
extent of nest-aggregation	33	0.23	> 0.10	
extent of food-aggregation	33	0.19	> 0.20	

Table 2. *Associations between changes in the frequency of mate desertion and changes in the costs and benefits of desertion among recent lineages, controlling for phylogeny*

(Regression models based on standardized independent contrast scores. All analyses performed on contrasts between recent lineages only (lower than between-family level according to the relevant phylogeny). Two independent phylogenies are used. All regressions are single least squares models forced through the origin. Frequency of mate desertion is the dependent variable in all models.)

independent variable	<i>N</i>	<i>r</i>	<i>p</i>	slope ($\pm$ s.e.)
(a) analyses based on molecular phylogeny				
direct fecundity-cost	4	—	—	
duration of chick-feeding period	26	0.07	> 0.50	
extent of nest-aggregation	26	0.53	< 0.01	58.05 ($\pm$ 18.41)
extent of food-aggregation	26	0.49	< 0.01	0.28 ($\pm$ 0.10)
(b) analyses based on morphological phylogeny				
direct fecundity-cost	4	—	—	
duration of chick-feeding period	25	0.29	> 0.50	
extent of nest-aggregation	25	0.48	< 0.01	47.97 ($\pm$ 17.96)
extent of food-aggregation	25	0.54	< 0.001	0.33 ($\pm$ 0.10)

aggregation. In this case there was significantly more variation among higher phylogenetic levels (82% among higher levels, $F_{1,94} = 5.5$, $p < 0.05$).

Frequency of mate desertion varied across all phylogenetic levels (figure 1*i-j*). For example, using the molecular phylogeny we found that 59% of the variation in the frequency of desertion occurred among higher levels, and using the morphological phylogeny we found the corresponding value to be 56%. In neither case is this pattern of variation significantly different from that expected by chance ($F_{1,95} = 1.7$, $p > 0.10$, and $F_{1,94} = 0.63$, $p > 0.40$, respectively).

(b) *Ecological correlates of desertion*

The ecological correlates of changes in the frequency of mate desertion were not consistent across all phylogenetic levels. Among ancient lineages changes in

the frequency of desertion were correlated with changes in the indices of the potential costs of desertion but not with the indices of the potential benefits of desertion. Increases in the frequency of desertion were associated with significant decreases in the direct fecundity-cost of desertion and shortening of the chick-feeding period (table 1). However, among recent lineages changes in the frequency of desertion were correlated with changes in the indices of the potential benefits of desertion but not with changes in the indices of the potential costs of desertion. Increases in the frequency of desertion are associated with significant increases in the extent of nest and food-aggregation (table 2). In the case of contrasts in direct fecundity costs among more recent phylogenetic lineages, few non-zero changes were identified and regression analysis were not helpful. Hence, with reference to recent lineages, our conclusion that changes in the frequency of mate desertion are not

morphological phylogeny, (e) variation in extent of nest-aggregation using the molecular phylogeny, (f) variation in extent of nest-aggregation using the morphological phylogeny, (g) variation in extent of food-aggregation using the molecular phylogeny, (h) variation in extent of nest-aggregation using the morphological phylogeny (i) variation in frequency of desertion using the molecular phylogeny, and (j) variation in frequency of desertion using the morphological phylogeny. Error bars show standard errors.

Table 3. *Proposed hierarchical view of the evolution of variation in mating system among birds*

level of variation	basis of variation	source of variation
between orders	} differences in costs of desertion	life history
between families		
between genera	} differences in benefits of desertion	ecology
between species		
between populations		
between individuals	differences in intra- and intersexual conflict	social interactions

correlated with changes in the costs of desertion is based only on data concerning the duration of the chick-feeding period. Both molecular and morphological phylogenies gave the same result.

4. DISCUSSION

Variation among species in either genotypic or phenotypic characteristics is due to episodes of diversification. However, not all such diversification necessarily occurred over the same period of time. Variation in some traits may be due to changes that occurred in the distant evolutionary past, while variation in other traits may be due to recent or ongoing change. For example, our analyses suggest that variation in traits associated with the costs of mate desertion is due largely to diversification that occurred in the ancient evolutionary history of birds, while variation in the frequency of mate desertion is due to repeated instances of diversification throughout avian history. These conclusions imply that variation in the costs of desertion cannot explain all variation in mate desertion. Variation in costs can only explain that portion of the variation in the frequency of desertion that occurs among ancient lineages. However, not all potential explanatory factors show the same pattern of variation across phylogenetic levels. Variation in traits associated with the benefits of desertion, like that in the frequency of desertion itself, was expressed across all phylogenetic levels. Together, these patterns suggest that variation in the frequency of mate desertion may be due to different ecological factors at different phylogenetic levels. This is why, when attempting to identify ecological correlates of variation in the frequency of mate desertion, we performed our analyses separately at different phylogenetic levels—firstly among ancient lineages, then among more recent lineages.

Our analyses of the ecological basis of mate desertion in birds confirm theoretical predictions (Maynard Smith 1977), that it is the interaction between the costs and benefits of mate desertion that is the crucial element in determining the likelihood of desertion, rather than either the costs or the benefits in isolation. Phylogenetic groups such as the Phasianidae may be predisposed to mate desertion because costs of desertion are low and periods of chick-feeding are short. This conclusion is consistent with Lack's understanding and with the work of Temrin and Sillén-Tullberg who, using a phylogenetic analysis of variation in mate desertion among avian families, found that the fre-

quency of mate desertion was positively correlated with short periods of chick-care and well-developed offspring (Sillén-Tullberg & Temrin 1994; Temrin & Sillén-Tullberg 1994, 1995). The outcome of our work is novel, however, in suggesting that desertion only actually occurs within these predisposed groups when local ecological conditions enhance the availability of additional mating opportunities. Indeed, we propose that the evolution of mating patterns among birds can be regarded as a hierarchical process (table 3), in which life history determines whether mate desertion is possible in a particular lineage, ecological conditions determine whether desertion is viable in a particular species or population, and social interactions (Davies 1989, 1992) determine whether the strategy will be adopted by a particular individual.

This hierarchical view of the evolution of avian mating systems may explain a number of otherwise puzzling observations. For example, it has been difficult to identify a general ecological correlate of social monogamy (e.g. Lack 1968; Wittenberger & Tilson 1980; Oring 1982; Davies 1991; Gowaty 1996). Our analyses suggest that this may be because phylogenetically distantly related species may display similar mating patterns for very different evolutionary reasons. For instance, in lineages which are 'constrained' to extensive parental care by the ancient evolutionary events which led to their extreme life-history strategy (see Owens & Bennett 1995), social monogamy may be obligatory and largely independent of local ecological and social conditions (e.g. shearwaters and albatrosses, Procellariidae). In other lineages, where life-history traits facilitate mate desertion, social monogamy is facultative and its expression is dependent on the local ecological or social conditions that limit the availability of additional mates (e.g. accentors; see Davies 1992; Davies *et al.* 1995). Thus, monogamy may arise via remarkably different evolutionary pathways.

A hierarchical view may also explain the empirical observations mentioned in the introduction. For instance, the reason why Webster (1991) found no relationship between the cost of desertion and the incidence of social polygamy may be that he only considered species from a few passerine lineages. We suggest that all of these lineages may be equally predisposed to polygamy and that differences between them in the incidence of polygamy are due to differences in the availability of additional mating opportunities rather than differences in the costs of desertion. We predict that manipulating the avail-

ability of mates would induce polygamy in many of the putatively monogamous species. Similarly, the finding that mate desertion can be induced in certain lineages by experimentally increasing the local availability of mates (Smith *et al.* 1982; Hannon 1985) may be due to the fact that, while certain lineages are predisposed to desertion, some species within these lineages are limited to monogamy by local ecological or social factors. We predict that such manipulations will lead to mate desertion in putatively monogamous species that are closely related to other species in which polygamy is common, but will not result in desertion when the study species has no close polygamous relatives.

Of course this hierarchical view is not entirely new. Lack knew that variation in the costs of desertion could not explain all mating system variations in birds and even guessed that, within certain taxa, variation in the benefits of desertion may also play a role.

It is more surprising to find that monogamy is the rule in many ducks and limicoline waders, in which only one parent incubates and cares for the young ... Presumably, even in such species, a male tends to leave more offspring if mated with only one female than with several. This will be helpful if the sex ratio is nearly equal, so that it is difficult to obtain more than one mate.

David Lack (1968), p. 150

Such subtleties were, however, difficult to incorporate into a general view and tended to be lost in future references. More explicit recognition of the dual importance of 'phylogenetic factors' and 'ecological potential for polygamy' and of the way they can interact can be found in the pioneering work of Emlen and Oring (1977) and Oring (1982). Our analyses simply demonstrate that, using modern comparative methods, 'phylogenetic constraints' can now be analysed in a quantitative fashion and their importance can be compared with that of contemporary ecological and social factors. We hope that the use of such analyses will lead to the general concept of 'phylogenetic constraint' being dismantled into more tractable constraints based on morphology, physiology, development and genetics.

5. CONCLUSIONS

Our analyses suggest that variation among birds in social mating systems is due largely to a combination of evolutionary predisposition and ecological facilitation. Certain lineages are predisposed to mate desertion through having a short chick-feeding period and low costs associated with desertion. However, within these predisposed lineages, desertion only actually occurs when the benefits of such behaviour are likely to be high. This type of hierarchical approach has previously been used to examine questions of both allometric scaling (Lande 1979; Martin & Harvey 1984; Bennett & Harvey 1987) and relative species-abundance (Nee *et al.* 1991). It remains to be determined whether a similar approach will prove useful in understanding the ecological basis of aspects of variation overlooked by the present analyses. For instance, better empirical data on variation among species in the costs and benefits of desertion may reveal the significance of

variation in (i) the exact stage in the breeding chronology at which desertion occurs, (ii) sex differences in the frequency of desertion, or (iii) the regularity of alternative reproductive strategies such as extra-pair copulation and egg dumping.

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