

Why care? Inferring the evolution of complex social behaviour

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Keywords:

birds;
 character evolution;
 parental care;
 parental investment;
 phylogenetic comparative methods;
 sex role.

Abstract

Phylogenetic comparative analyses of complex traits often reduce the traits of interests into a single (or a few) component variables. Here, we show that this may be an over-simplification, because components of a complex trait may evolve independently from each other. Using eight components of parental care in 400 bird species from 89 avian families that represent the relative contribution of male vs. female to a particular type of care, we show that some components evolve in a highly correlated manner, whereas others exhibit low (or no) phylogenetic correlation. Correlations were stronger within types of parental activity (brooding, feeding, guarding) than within stages of the breeding cycle (incubation, pre fledging care, post-fledging care). A phylogenetically corrected cluster analysis identified two groups of parental care components that evolved in a correlated fashion: one group included incubation and brooding, whereas the other group comprised of the remaining components. The two groups of components provide working hypotheses for follow-up studies to test the underlying genetic, developmental and ecological co-evolutionary mechanism between male and female care. Furthermore, the components within each group are expected to respond consistently to different ambient and social environments.

Introduction

Parental care is a complex social behaviour that occurs in a large number of invertebrates and vertebrates (Wilson, 1975; Clutton-Brock, 1991; Balshine-Earn *et al.*, 2002; Reynolds *et al.*, 2002; McGraw *et al.*, 2010; Royle *et al.*, 2012). There is immense variation among species in type of care, in care behaviours associated with different stages of offspring development and in the relative contribution of males and females to care. Understanding this diversity is one of the fundamental objectives in evolutionary biology, because parental care is related to life histories and ecology of organisms, and to the evolution of sex roles and breeding systems (Houston *et al.*, 2005; Alonso, 2010; Jennions & Kokko, 2010; Smiseth *et al.*, 2012).

Like many behaviours, parental care is complex because it comprised of multiple behavioural compo-

nents (Silver *et al.*, 1985; Gardner & Smiseth, 2011). To understand the evolution of such behaviour requires that we dissect out the evolution of a suite of different correlated traits. On the one hand, different components of care (e.g. gestation, lactation, brood defence) may coevolve as a single unit, given that selection most likely acts on the outcome of all of these components: parental fitness. On the other hand, components of complex traits may have different genetic, developmental and neuro-endocrine pathways (Adkins-Regan, 2005; Sokolowski & Levine, 2010), and gene expressions in different parts of the brain may only target specific components of a behaviour (Blumstein *et al.*, 2010; O'Connell & Hofmann, 2012). If these genetic, physiological and/or developmental mechanisms manifested separately for each component, this would produce poorly correlated evolution between components of complex traits (Ord & Martins, 2006; Erdtmann & Amezquita, 2009; Ord, 2010).

Here, we use avian parental care to investigate complex trait evolution. Birds are often used as model organisms to understand parental care evolution (Ben-

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nett & Owens, 2002; Cockburn, 2006; Smiseth *et al.*, 2008; van Dijk & Székely, 2008; McGraw *et al.*, 2010; Gardner & Smiseth, 2011). However, previous phylogenetic analyses of parental care often treated care as a single trait (Székely & Reynolds, 1995; Owens & Bennett, 1997; Cockburn, 2006), and this broad-brush categorization may conceal much of variation that natural selection may act upon (Webb *et al.*, 2010; Smiseth *et al.*, 2012). Treating complex traits have implications beyond semantics: recent models show that if care is modelled as a multivariate trait (and not as a single trait as most care models have performed so far), then task specialization evolves (i.e. one parent evolves doing one task best, whereas the other parent evolves doing another task best), and the task specialization stabilizes parental cooperation (Lessells, 2012; Harrison, F., T. Székely, A. Liker & Z. Barta, unpublished).

Using the largest and taxonomically broadest detailed dataset on parental care available for any group of organisms (400 bird species from 89 avian families and eight components of care), we have three objectives. Firstly, using care traits, we investigate two scenarios of care component evolution. On the one hand, correlated evolution of care components is expected for behaviours that are executed during a particular stage of care provisioning; for instance, chick feeding and brood defence are expected to exhibit high phylogenetic correlation given that the parents exhibiting one of these traits during brood development also have opportunity for providing the other. On the other hand, functionally similar behaviours are expected to exhibit more correlated evolution than dissimilar behaviours; for instance, nest defence during incubation may exhibit high correlation with nest defence during brood care, because these activities may involve similar physical and perception skills, and common regulatory mechanisms.

Secondly, we explore whether the demand of the young (precocial vs. altricial chicks, Starck & Ricklefs, 1998) influences the strength and direction of relationship between care traits. One may expect higher correlation across stages for altricial taxa than for precocial ones, because in the former, all aspects of pre-fledging care take place in a single environment (i.e. at or around the nest), whereas in precocial species, the parents (and their chicks) are exposed to variable environments given that some of chick development takes place away from the nest. Thirdly, we explore the relationships between parental care components (or care traits), to provide working hypotheses for follow-up studies. For instance, a finding that incubation behaviour and chick brooding are highly correlated across avian taxa would suggest that the genetic and/or developmental mechanisms underlying these two traits are extensively shared.

Our initial premise was to investigate care estimates separately for males and females (e.g. time spent by male and females on each parental activity). However,

data in the literature are not sufficiently consistent across vast majority of species to allow separate care estimates for males and females. Therefore, we followed previous studies (Silver *et al.*, 1985; Møller & Cuervo, 2000; Arnold & Owens, 2002) and scored the relative contribution of male and female to a particular care type (see Methods). Therefore, care components represent the degree of male's time allocation relative to female's time allocation in each of the eight components.

Materials and methods

Data collection

Data on eight parental care traits were collected from handbooks and primary publications: nest building, incubation, nest guarding, chick brooding, chick feeding, chick guarding, post-fledging feeding of chicks and post-fledging guarding of chicks. These variables were straightforward to recognize in the ornithological literature (see also Liker & Székely, 2005 for a similar division of avian parental care). Data were extracted by one observer (AL). Because continuous data were not available for many species, we scored the relative participation by males on a 5-points scale for each care component separately (0: no male care, 1: 1–33% male care, 2: 34–66% male care, 3: 67–99% male care, 4: 100% male care). Where quantitative data were not available, we used suitable verbal statements to score the participation of the sexes between 0 and 4. For example, in species in which 'most incubation is provided by females', we gave an incubation score 3 for females and score 1 for males. In this scoring system, the estimates of male and female participation in care are completely dependent, that is, female scores would always be the reverse of male scores (4-0, in the above order), and the separate scores of the sexes would always add up to 4 for a given type of care. As a consequence, an evolutionary increase in a score may represent either an evolutionary increase in male care, or a decrease in female care, or both. For some of these traits, for example, incubation and brooding where usually only one parent can provide the care at any given time, an increase in care by one parent should be associated with decrease by the other, thus increases in male scores mean increased male participation. We did not find information on all care traits for all species, thus sample sizes differ between analyses.

We split breeding activity into three main phases: (i) pre-hatching that includes nest building and care of the eggs before the chicks hatch, (ii) pre-fledging care: after the chicks hatch and before they leave the nest (in altricial species, see below), or before they fledge (in precocial species) and (iii) post-fledging care that includes post-fledging feeding and brood guarding. We divided the eight care traits into three functional groups: (i) direct nest and offspring care that included

nest building, incubation and chick brooding, (ii) the feeding of offspring that included chick feeding and post-fledging feeding and (iii) defending offspring that included nest guarding, chick guarding and post-fledging guarding. We follow Olson *et al.* (2008) to allocate species to 'precocial' and 'altricial' developmental modes. Using a finer-scaled grouping would have resulted in fewer species in each group, and thus we opted for a dichotomous variable.

Phylogenetic analyses

We used male share in eight different parental traits as response variables in the phylogenetic analyses. First, we focus on bivariate relationships, and then analyse multiple traits using cluster analyses and principal component analyses (PCA). Finally, we test the strength of phylogenetic signals.

Bivariate correlations between parental variables were tested using phylogenetic generalized least squares (PGLS, Hansen & Martins, 1996; Pagel, 1997; Freckleton *et al.*, 2002). In each bivariate model, only those species were included for that at least some care was provided either by the male or the female; for example, species in which neither the male nor the female feed the chicks (e.g. most precocial species) were not included in bivariate analyses of chick feeding trait.

Phylogenetic generalized least squares models were fitted using code written by RPF in R and available via the CAPER package (D. Orme, in review; Pagel, 1999; Freckleton *et al.*, 2002). Because no complete

molecular phylogenetic hypothesis is available that includes all species in our analyses, we compiled a composite phylogeny using Ericson *et al.* (2006) and Barker *et al.* (2004) for nonpasserines and passerines, respectively. Because these phylogenies only resolved relationships at family level and above, for within family relationships, we used specific publications (see Appendix 1). Branch lengths were not available for the composite tree; therefore, we estimated branch lengths by the Nee's method as implemented in Mesquite 2.74 (Purvis, 1995; Maddison & Maddison, 2010). In the PGLS models, the initial branch lengths were adjusted according to λ statistics estimated for each pair of parental care traits (Freckleton *et al.*, 2002).

We carried out the analyses using six sets of the data: (i) All species included in the analyses. (ii) Because in uniparental species male contribution is uniformly 0 (or 4) across all care traits, we repeated the analyses using only biparental species, defined here as species with both sexes participating at least in one care trait (Appendix 2). In the latter analyses, species in which a single parent carried out all care ($n = 58$ species, henceforth 'uniparental species') were not included. (iii) Precocial species only and (iv) altricial species only using the definition of Olson *et al.* (2008) (Appendix 2). Finally, we repeated the latter analyses using only biparental species separately for (v) altricial and (vi) precocial species (Appendix 3). Following Harper (1994), we interpret correlation coefficients as low correlation ($r < 0.4$), moderate correlation ($0.4 \leq r \leq 0.7$) and high correlation ($r > 0.7$, Tables 1 and 2).

Table 1 Bivariate relationships (controlled for phylogeny) between different care traits.

	Nest building	Incubation	Chick brooding	Nest guarding	Chick guarding	Post-fledging guarding	Chick feeding	Post-fledging feeding
Nest building		0.419*** 340	0.437*** 304	0.301*** 121	0.321*** 217	0.607*** 26	0.180** 267	0.276*** 149
Incubation	0.267*** 298		0.684*** 348	0.380*** 136	0.503*** 249	0.699*** 31	0.393*** 309	0.210** 169
Chick brooding	0.325*** 272	0.532*** 306		0.503*** 128	0.613*** 233	0.733*** 30	0.264*** 269	0.137 ^{NS} 162
Nest guarding	0.183 ^{NS} 110	0.178* 124	0.317*** 117		0.758*** 124	0.760*** 15	0.276* 82	0.222 ^{NS} 54
Chick guarding	0.123 ^{NS} 190	0.219** 213	0.394*** 204	0.625*** 112		0.978*** 28	0.562*** 162	0.418*** 104
Post-fledging guarding	-0.523* 19	0.158 ^{NS} 22	0.470* 22	0.331 ^{NS} 12	0.933*** 19		0.741*** 18	0.638* 13
Chick feeding	-0.089 ^{NS} 242	0.186** 276	0.058 ^{NS} 246	0.019 ^{NS} 78	0.233** 149	-		0.636*** 169
Post-fledging feeding	0.100 ^{NS} 140	0.041 ^{NS} 159	-0.024 ^{NS} 152	0.001 ^{NS} 52	0.080 ^{NS} 99	-	0.333*** 159	

PGLS, phylogenetic generalized least squares.

Each cell shows the phylogenetically corrected r , its significance (NS, * < 0.05 , ** < 0.01 , *** < 0.001) and the number of species. Significance levels are only provided for an illustrative purpose. Above diagonal: all species included, below diagonal: only biparental species included. Shading indicates correlation coefficients 0.4–0.7 (light grey) and > 0.7 (dark grey). Dash indicates variable pairs where PGLS failed to converge.

Table 2 Bivariate relationships (controlled for phylogeny) between different care traits separately for precocial and altricial species.

	Nest building	Incubation	Chick brooding	Nest guarding	Chick guarding	Post-fledging guarding	Chick feeding	Post-fledging feeding
Nest building	█	0.615*** 107	0.510*** 97	0.467** 61	0.434*** 96	0.721** 15	0.550*** 35	–
Incubation	0.287*** 233	█	0.714*** 112	0.540*** 69	0.641*** 115	0.866*** 18	0.828*** 41	–
Chick brooding	0.404*** 207	0.732*** 236	█	0.700*** 62	0.812*** 100	0.940*** 17	0.852*** 33	–
Nest guarding	0.107 ^{NS} 60	0.145 ^{NS} 67	0.229 ^{NS} 66	█	0.758*** 66	–	0.807*** 15	–
Chick guarding	0.170 ^{NS} 121	0.252** 134	0.381*** 133	0.767*** 58	█	0.977*** 18	0.954*** 28	–
Post-fledging guarding	0.375 ^{NS} 11	0.258 ^{NS} 13	0.226 ^{NS} 13	–	1.0 10	█	–	–
Chick feeding	0.127 ^{NS} 232	0.302*** 268	0.136* 236	0.018 ^{NS} 67	0.351*** 134	0.334 ^{NS} 13	█	–
Post-fledging feeding	0.285*** 146	0.231** 166	0.179* 159	0.223 53	0.420*** 102	0.640* 12	0.632*** 166	█

Each cell shows the phylogenetically corrected r , its significance (NS, * < 0.05 , ** < 0.01 , *** < 0.001) and the number of species. The significance levels are only provided for an illustrative purpose. Above diagonal: precocial species, below diagonal: altricial species. Both biparental and uniparental species were included in the models. Shading indicates correlation coefficients 0.4–0.7 (light grey) and > 0.7 (dark grey). Dash indicates < 10 species and also the lack of post-fledging feeding in precocial birds.

Comparisons of correlation coefficients between functional groups and stages of care (see Results) were carried out by one-way analyses of variance using permutation test ('aovp' function in the 'lmPerm' R package, R 2.9.2; R Development Core Team, 2009). We used permutation because pairwise correlation coefficients are not independent from each other. To check the robustness of the results, all tests were repeated using the lower and upper confidence estimates of the correlation coefficients. Pairwise differences between groups were tested by Tukey HSD tests using parametric ANOVA because we are not aware of an equivalent procedure based on permutation. Note that the parametric and permutation-based ANOVAs produced fully consistent results.

Cluster analyses were carried out to test the associations between different forms of care behaviour. We treated care traits as the elements to be grouped and to control for phylogenetic dependence, first, we transformed the data and then used the transformed data in cluster analyses. We used a transformation suggested by Garland & Ives (2000) and Wood (2006), that renders the data independent of phylogeny, and data can then be used in conventional analyses with no further regard for phylogenetic dependence. We used the 'dist' function in the 'stats' R package to calculate Euclidean distance matrices and 'hclust' function to perform hierarchical clustering using Ward's method. Similarly, PCA were carried out using the phylogenetically transformed parental care scores, using 'rda' function in the 'vegan' package.

Cluster analyses and PCA were carried out using 6 (or 7) care traits, because sample sizes rapidly decreased due to missing data in one (or several) traits. Post-fledging guarding was not included in the latter

analyses due to large number of missing data. Note that because chick feeding was included in the cluster analyses and the PCAs, these analyses only included species in which the parents feed the chicks (altricial birds and two precocial species).

To calculate phylogenetic signal, we used two methods. First, λ statistics were calculated separately for each care trait by the PGLS (using the method described in Freckleton *et al.*, 2002; see above). Second, we used a new likelihood estimation method that simultaneously estimates separate values of λ for several traits and can perform fast calculations for large phylogenies (Freckleton, in press). The potential advantage of the latter approach is that the values of λ account for the interrelationships of the traits, whereas the simpler approach of calculating λ for each trait separately ignores this structure in the data. The disadvantage is that, because in this analysis λ s were simultaneously estimated for all care traits, we could only use species without missing care data ($n = 41$ species; without post-fledging guarding that had a large number of missing data).

The minimum and maximum values of λ are 0 and 1, respectively; 0 indicates that the evolution of traits is independent from the phylogeny, whereas 1 indicates that traits are evolving according to Brownian motion on the given phylogeny.

Results

Evolution of care components

Most correlations between components of care were positive, and 17 of 28 relationships were highly (or

moderately) correlated (Fig. 1, Table 1). Those that exhibited high correlations included nest guarding and chick guarding, whereas those that tended to have lower correlations included nest building and post-fledging feeding (Fig. 1). Uniparental species contributed substantially to the high correlations in Table 1, because by excluding the uniparental species from the analyses, only five of 28 relationships remained highly (or moderately) correlated (Table 1).

Care components that have similar functions (see Methods) exhibited high correlations (for instance, incubation and chick brooding, and nest guarding and chick guarding, Fig. 2a). In contrast, components of care performed during the same stage of breeding (for instance, incubation and nest guarding; chick brooding and chick feeding), and those components that neither had similar function nor were carried out during the same stage of development had lower correlations (permutation-based one-way ANOVA, d.f. = 2, 25, $P = 0.035$; using lower and upper confidence estimates of correlation coefficients: $P_{\text{lower}} = 0.004$, $P_{\text{upper}} = 0.096$), with the only significant pairwise difference was between the first and last groups (Tukey HSD, $P = 0.025$). The latter results remained highly significant when only biparental species were included in the models (permutation-based one-way ANOVA, d.f. = 2, 23, $P = 0.001$; $P_{\text{lower}} = 0.006$, $P_{\text{upper}} = 0.016$; Tukey HSD: $P = 0.003$; Fig. 2b).

Precocial vs. altricial species

Unexpectedly, precocial species exhibited higher correlations in care traits than altricial species (Fig. 2a, Table 2; matched pairs t -test, $t = 7.5$, d.f. = 17, $P < 0.001$; $t_{\text{lower}} = 6.2$, $P_{\text{lower}} < 0.001$, $t_{\text{upper}} = 7.0$, $P_{\text{upper}} < 0.001$). This result remained consistent with repeating the analyses using only biparental species (Fig. 2b, matched pairs t -test, $t = 4.1$, d.f. = 16, $P < 0.001$; $t_{\text{lower}} = 3.5$, $P_{\text{lower}} = 0.002$, $t_{\text{upper}} = 4.5$, $P_{\text{upper}} < 0.001$).

In precocial species, correlations between different functional groups of variables were not significantly different (Fig. 2; permutation-based one-way ANOVA, d.f. = 2, 15: $P = 0.782$, $P_{\text{lower}} = 0.816$, $P_{\text{upper}} = 0.612$; precocial biparental species only, d.f. = 2, 14: $P = 0.784$, $P_{\text{lower}} = 0.175$, $P_{\text{upper}} = 0.882$).

In altricial birds, correlations between care traits with similar functions were significantly higher than those in the other two groups (breeding stage and the remaining traits, see Fig 2; permutation-based one-way ANOVA, d.f. = 2, 15: $P < 0.001$; altricial biparental species only: $P = 0.003$), although the latter results were no longer significant using the upper confidence estimates of the correlation coefficients (breeding stage and neither, see Fig 2; permutation-based one-way ANOVA, $P_{\text{lower}} = 0.003$, $P_{\text{upper}} = 0.174$; altricial biparental species only: $P_{\text{lower}} < 0.001$, $P_{\text{upper}} = 0.170$).

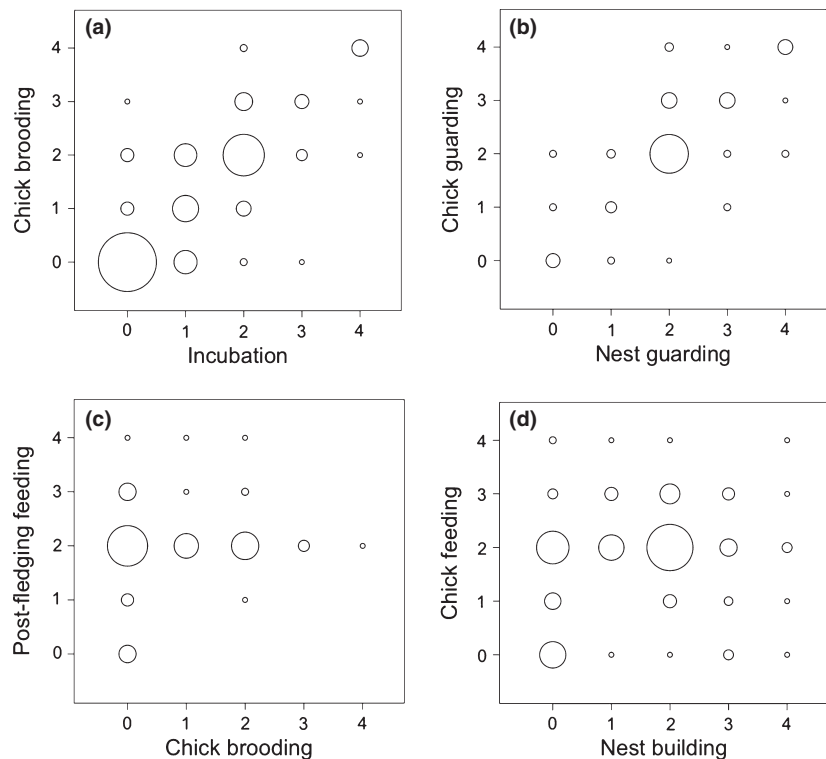


Fig. 1 Examples of strong correlation (a, b) and weak correlation (c, d) between parental care traits (all species included; see the phylogenetically corrected statistics in Table 1; $n = 348$, 124, 162 and 267 species in a, b, c and d, respectively). The circle size is proportional to the square root of the number of cases.

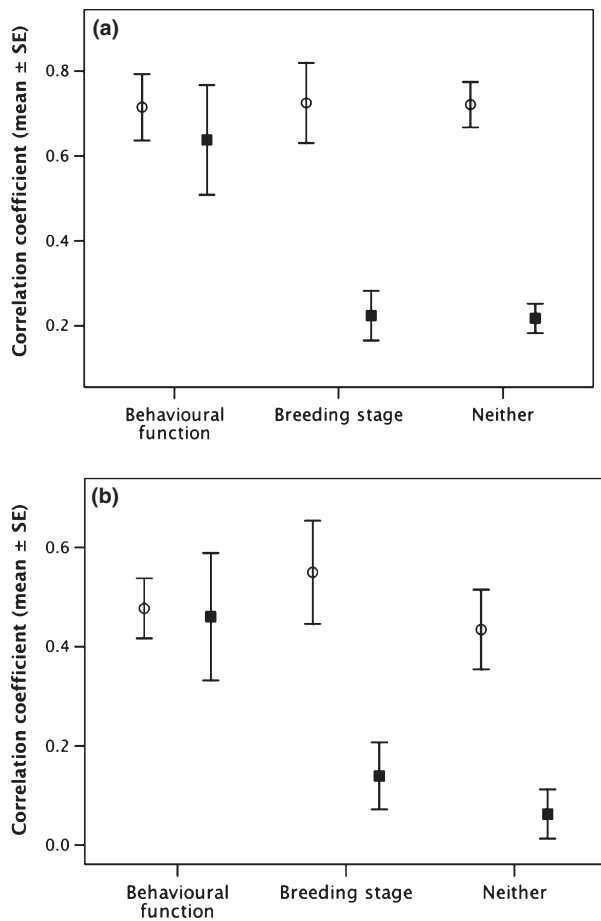


Fig. 2 Phylogenetically corrected correlation coefficients among parental care traits in precocial (open circles) and altricial species (filled squares). (a) all species, (b) biparental species only (see text for statistics).

Phylogenetic structure of parental care traits

Functionally similar care traits clustered together (Fig. 3), consistently with the aforementioned bivariate correlations. The cluster analyses identified two groups of traits: one group comprised of nest building, incubation and chick brooding (direct care), and the other group comprised of the remaining traits. Interestingly, the nest building-incubation-brooding group remained highly separated from the other components in both analyses using different number of traits and species (Fig. 3).

These results remained consistent with phylogenetically corrected PCA. The cumulative variance explained by PC1 and PC2 in analyses of six and seven care traits was 33% and 29%, respectively. The second PCA separated the traits into direct care (incubation, brooding and nest building) and the rest of traits (Fig. 4, Table 3). Some of the species that exhibit extreme

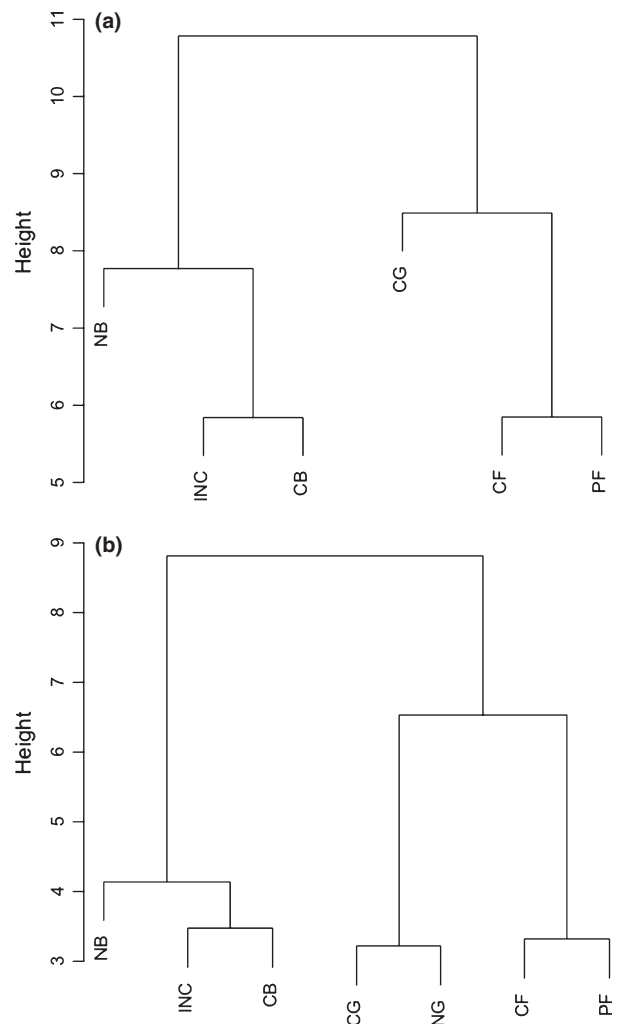


Fig. 3 Phylogenetically corrected cluster analyses using (a) six traits (93 species) and (b) seven traits (41 species). Nest building (NB), Incubation (INC), Chick brooding (CB), Nest guarding (NG), Chick guarding (CG), Chick feeding (CF), Post-fledging feeding (PF). Height indicates dissimilarity between traits.

values are given on Fig. 4. These results remain consistent by restricting the analyses to biparental species only (Appendix 3).

Most traits exhibited high phylogenetic signals as indicated by high λ values, although significantly different from one (predicted by Brownian motion) for nearly all traits, and the two methods (see Methods) produced consistent λ estimates (Table 4). This is an important finding, because it suggests that male and female division of care co-evolved and has retained a significant phylogenetic signal.

Discussion

Individual components of a complex social behaviour, such as parental care, do not evolve in isolation from

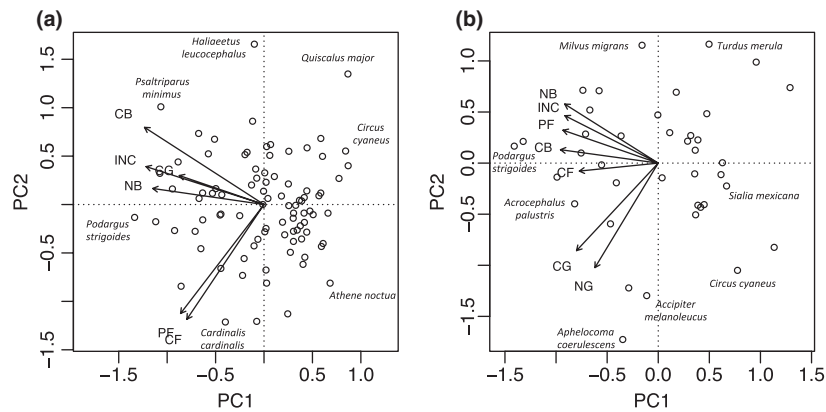


Fig. 4 Phylogenetically corrected one principal component analyses using (a) six traits (93 species) and (b) seven traits (41 species). The arrows show the relative loadings of the care traits on the first and second principal components, whereas circles show the position of individual species; the figures are scaled to show unbiased relative values for the care traits. Nest building (NB), Incubation (INC), Chick brooding (CB), Nest guarding (NG), Chick guarding (CG), Chick feeding (CF), Post-fledging feeding (PF).

Table 3 Phylogenetically corrected principal component analyses (PCA) showing factor loadings using six or seven parental care traits ($n = 93$ and 41 species, respectively). Loadings are Pearson correlation coefficients between the trait and PCA factors (PCA1 or PCA2).

Parental care trait	6 traits		7 traits	
	PCA1	PCA2	PCA1	PCA2
Nest building	-0.409	0.246	-0.353	-0.431
Incubation	-0.434	0.335	-0.337	-0.497
Chick brooding	-0.425	0.488	-0.354	-0.371
Chick feeding	-0.380	-0.542	-0.397	0.293
Chick guarding	-0.389	-0.071	-0.408	0.338
Post-fledge feeding	-0.409	-0.539	-0.432	0.063
Nest guarding	-	-	-0.356	0.476

each other or from the rest of the phenotype (Ord & Martins, 2006; Smiseth *et al.*, 2012). Here, we focus on the correlated evolution between components of a complex social behaviour, and using male share in eight care traits, we show that parental behaviour is made up of several components, each differing in the propensity for evolutionary change.

Our analyses provided three key results: care components do not necessarily co-evolve with each other, they cluster in two groups, and several components have high phylogenetic signals. These results remain robust whether we included both biparental and uniparental species in the analyses, or only biparental ones. Firstly, we showed that parental care components, that is, the relative role of sexes in care components, do not necessarily evolve in a coordinated manner. Thus, some aspects of male and female involvement in care co-evolve, whereas others do not. Those that had the highest correlated evolution were the ones that are functionally close. Thus, avian

Table 4 Phylogenetic signal (λ) of single care traits estimated by PGLS in which values of lambda are estimated separately from each trait (λ_{PGLS}) and a new likelihood method in which values of lambda are estimate for all traits simultaneously (λ_{lik}). For λ_{PGLS} , the probability that λ is different from 0 or 1 and the number of species (n) included in model fitting are given; using Nee's branch lengths provided better fit (ΔAIC) than using unit branch lengths. In the calculation of λ_{lik} , sample size was 41 species, and it was not estimated for post-fledging guarding due to the large number of missing data.

Parental care trait	λ_{PGLS}	Difference of λ_{PGLS} from			ΔAIC	λ_{lik}
		0	1	n		
Nest building	0.902	< 0.001	0.003	342	13.5	1.000
Incubation	0.895	< 0.001	< 0.001	398	25.8	0.811
Nest guarding	0.418	0.089	< 0.001	138	5.6	0.000
Chick brooding	0.899	< 0.001	0.012	348	42.8	0.715
Chick feeding	0.545	< 0.001	< 0.001	309	25.5	0.563
Chick guarding	0.649	< 0.001	< 0.001	249	25.8	0.417
Post-fledge feeding	0.331	0.138	< 0.001	169	27.0	0.000
Post-fledge guarding	1.000	< 0.001	1.000	31	5.9	-

PGLS, phylogenetic generalized least squares.

parental behaviour is constituted from multiple components: some are highly dependent, whereas others are semi-independent of each other, with each trait potentially targeted by different forms of selection by the social and physical environment, or by other factors (Wilson, 1975; McGraw *et al.*, 2010; Gardner & Smiseth, 2011; Smiseth *et al.*, 2012). Consistent with our results, territorial displays cluster into 5 trait complexes in *Anolis* lizards: with high correlations between cluster members and weaker across members of different traits (Ord & Martins, 2006). Although the number of clusters differs between lizards and birds as one might expect, both works suggest that certain compo-

nents of behaviour (territorial display in lizards and relative care contribution in birds) are co-evolving and robust over evolutionary time, whereas others are not. The high correlations can give rise to suites of traits, and selection can act simultaneously on these suites of behavioural traits (Bell, 2005; Moretz *et al.*, 2007). There are few intraspecific studies on individual consistencies between different care traits, but these also suggest that parents behave consistently for some set of care behaviour (e.g. take a large share in all of them) but not for others (Hoi *et al.*, 2003; Kopisch *et al.*, 2005).

Overall, the parental care components exhibited higher correlated evolution in precocial taxa than in altricial taxa, and the difference between precocial and altricial species remained highly significant by restricting the analyses to biparental species. This is somehow surprising, because one would expect that correlated evolution would be higher among altricial species due to the similar selection pressure to feed the young for an extended period. This novel result also suggests that the more dependent young in altricial species opens up different phylogenetic trajectories in care, rather than restricting them. One potential explanation for this paradox may be that natural selection invented different pathways between different avian lineages to respond to the more demanding offspring. Another argument would be that by providing substantial care for the young in altricial species, the female can copulate with (and induce) several males to contribute to care provisioning (Møller & Cuervo, 2000; Houston *et al.*, 2005); however, frequent extra-pair copulations may result in reduced male care in some care behaviour (Møller & Cuervo, 2000; Matysioková & Remeš, 2013). This would make mating systems and parental care more plastic and dynamic in altricial species by lowering the evolutionary correlations between care components.

Secondly, traits are often linked to each other developmentally, physiologically or genetically. Our analyses identified two clusters of care components: one cluster comprises incubation of eggs and brooding of the young, and nest building. All other care traits ended up in the other cluster. This clustering is consistent with principal component analysis and suggests that the genetic and/or physiological mechanisms of these behaviours within the two groups may be regulated by similar mechanisms. In line with our results, Møller & Cuervo (2000) found that male share in nest building correlated with his involvement in incubation, although neither of these was related to male share in feeding young.

To further test the shared genetic, developmental or hormonal mechanisms underlying male share in parental care (Adkins-Regan, 2005), researchers will need to experimentally alter the expression of relevant genes (or gene expression pathways) involved in producing the complex trait (Robinson *et al.*, 2008; Blumstein

et al., 2010). A testable prediction of our study is that perturbing gene expression and/or developmental pathways underlying parental behaviour, the corresponding changes will be stronger in traits within each cluster, than between traits in different clusters. Our approach therefore has implications for predicting how complex traits may respond to environmental or social selective forces and has the potential for linking phylogenetic approaches to studies of contemporary adaptation (Losos, 2011). According to this prediction, the few studies that investigated the effects of experimental hormonal manipulations on multiple care traits in the same species suggest differences in the endocrine regulation of different types of parental behaviour (Ketterson & Nolan, 1992; Cawthorn *et al.*, 1998; Schwagmeyer *et al.*, 2005).

Thirdly, we found that several of these behavioural traits contained high phylogenetic signals, particularly the component of direct care ($\lambda = 0.7\text{--}1.0$). These results were robust in terms that (i) they were consistent between two estimation methods and (ii) did not depend strongly on the particular set of species (in the analysis using the likelihood method we used a subset of taxa and same species for all care traits). Phylogenetic signals are typically high in advertisement calls in frogs and lizards (Ord & Martins, 2006; Erdmann & Amezcuita, 2009), and high in relative contribution of male to care in birds (Matysioková & Remeš, 2013; this study). This suggests that not only mating display, the trait well known to exhibit strong phylogenetic signals (Lorenz, 1941), but also parental care contains substantial phylogenetic signal. This conclusion is consistent with laboratory-based analyses of parental behaviour that showed high genetic correlation between different aspects of care (Walling *et al.*, 2008), although somehow surprising because parental care in wild populations usually seen as largely moulded by environment (Wilson, 1975; Brown *et al.*, 2010; AlRashidi *et al.*, 2011).

A limitation of our study is, however, that the traits represent relative involvement of males in parental behaviour. As we explain in the Methods, scoring the relative investment of sexes was a necessity dictated by data availability, rather than our preference. One implication of the current study therefore is that the high co-evolution between traits can be driven by corresponding changes in males, females or in both sexes. To distinguish between these scenarios, one needs to quantify male and female care separately that may be feasible for a subset of species. However, for some components of care, our scoring reflects absolute contributions to care, for example, because males can only increase their incubation if females decrease theirs. In addition, experimental manipulations of one parent showed that the other parent compensated the lost care in most contemporary populations, suggesting the two parents also trade-off in

other forms of care, for example, in chick feeding (Harrison *et al.*, 2009).

Evolutionary studies of social behaviour are rapidly advancing thanks to the advent of vast amount of data generated by next generation sequencing, technical advances in neuro-genomics and statistical approaches in phylogenetic comparative analyses (Robinson *et al.*, 2008; Adkins-Regan *et al.*, 2010; Freckleton & Pagel, 2010; Young & Flanagan-Cato, 2012). The evo-devo approach to social behaviour has been successful picking up candidate genes and neuro-pathways that have been linked to various social traits (Robinson *et al.*, 2008; Goodson *et al.*, 2012). To reveal the complex network of gene expressions, developmental pathways and phenotypes, however, it is important to set *a priori* predictions how phenotypic traits may be related. This is one of the major objectives of our current study in the context of the relative role of sexes in care components. So from this perspective, our study is important for generating new hypotheses using behavioural data from across 400 different bird species using a phylogenetic approach. We are aware that few evolutionary biologists have yet used this approach; nevertheless, the data and techniques are fully available to use a similar approach in other phenotypic traits, including behaviour.

In conclusion, we show that parental care is a complex trait: some aspects of care co-evolve more than others. This grouping can give rise to traits that selection act upon in a consistent way and suggest specific groups of traits that can be experimentally manipulated. Further phylogenetic analyses of care are desirable in taxa that exhibit highly variable care behaviour, for instance, assassin bugs, bony fishes and tropical frogs, and primates (McGraw *et al.*, 2010). Finally, the analyses we present here may open new research opportunities by linking phylogenetic analyses to studies of contemporary populations in genetics, development and adaptation.

Acknowledgments

We acknowledge the comments of Per Smiseth and Andy Gardner on previous versions of this manuscript. TSz was funded by the European Community's Sixth Framework Programme (FP6/2002-2006) under contract n. 28696 (GEBACO) and FP6-2005-NEST-Path, no. 043318 (INCORE). AL was supported by a Marie Curie Intra-European Fellowship. RPF is funded by a Royal Society University Research Fellowship. VR was supported by Palacky University (IGA PrF_2012_021).

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The phylogenetic hypothesis used in comparative analyses of avian parental care, in Newick tree format.

Appendix S2 Species included in the analyses, devel-

opment mode (precocial or altricial), and parental care type (uniparental or biparental).

Appendix S3 Analyses based on biparental species only.

Received 5 May 2012; revised 21 December 2012; accepted 3 February 2013