Life history evolution in cichlids 1: revisiting the evolution of life histories in relation to parental care

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Abstract

Empirical links between egg size and duration of parental care in fishes have generated a considerable amount of theory concerning life history evolution. However, to date, this link has not been investigated in relation to other important life-history traits such as clutch size and body size, or while controlling for shared ancestry between species. We provide the first phylogenetically based tests using a database with information on egg size, clutch size, body size and care duration in cichlid fishes (*Cichlidae*). Multiple regression analyses, based on independent contrasts on both the species and the genus level, showed that clutch size is the variable most closely related to duration of care. This pattern appeared to be driven by post-hatch care relationships. Our results show that, contrary to expectation, there is no positive link between egg size and care duration in *Cichlidae*. Instead, greater reproductive output through increased clutch size investment appears to have coevolved with greater care of offspring. We suggest that re-evaluation of the generality of current models of the evolution of egg size under parental care in fishes is needed.

Introduction

The optimal amount of resources that parents should invest into parental care depends strongly on the strength of the trade-off between reproductive events (Winkler, 1987; Clutton-Brock, 1991). This trade-off, in turn, depends on costs and benefits of care, which creates strong links between the levels of care and the life histories of taxa. Uncovering the link between important life histories and parental care may thus provide insights regarding the evolution of parental care and, ultimately, why the level of care is highly diverse among species.

Here we focus on three of the most important life-history traits that are believed to be linked to reproductive output in general, and parental care in particular: body size, clutch size and egg size (e.g. Roff, 1992; Stearns, 1992). All three of these traits have individually

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been suggested to affect parental care behaviours in accordance with life-history theory and this is particularly the case for care duration, one of the most commonly-used measures of parental care (e.g. Clutton-Brock, 1991). For instance, duration of care devoted to a given clutch size decreases with increasing body size in female convict cichlids, *Cichlasoma nigrofasciatum* (Galvani & Coleman, 1998). This was suggested to result from larger females gaining relatively less from protecting a small clutch as compared to the gains for small females. Clutch size or brood size has been shown to be positively associated with care duration within species in mammals, birds and fish (e.g. Clutton-Brock, 1991 and references therein).

Egg size has been shown to be positively correlated to parental care duration in various ectotherms (Shine, 1978; Gross & Sargent, 1985; Sargent *et al.*, 1987, Clutton-Brock, 1991). Particular interest in this phenomenon has been shown by studies of fishes where a strong positive correlation between egg size and care duration has been reported (e.g. Shine, 1978; Gross & Sargent, 1985; Sargent *et al.*, 1987). Several potential explanations

have been suggested to explain this correlation (Shine, 1978; Gross & Sargent, 1985; Sargent *et al.*, 1987; Nussbaum & Schultz, 1989; Shine, 1989). For instance, egg size may increase in response to an increase in care because larger eggs have longer development times, which can be spent in the 'safe harbour' of the care-giver (Shine, 1978; Sargent *et al.*, 1987). However, the opposite direction of causation has also been suggested. That is, selection for larger egg size could lead to selection for increased care due to greater parental demands from larger eggs (Nussbaum, 1985; Nussbaum & Schultz, 1989). Finally, this positive correlation may be explained by selection for a different trait that is strongly correlated to the two (Nussbaum & Schultz, 1989). One such trait may be body size, if body size is positively correlated to both egg size (e.g. Heath & Blouw, 1998) and care duration (e.g. Cooke *et al.*, 2002).

More work is needed before we can fully determine the ultimate explanation behind any co-variation between egg size and care in fishes (Clutton-Brock, 1991; Einum & Fleming, 2002). One first step towards understanding selection that has produced this correlation is to investigate how body size and clutch size, both important factors behind the evolution of egg size (e.g. Hendry *et al.*, 2001; Sakai & Harada, 2001) affect the correlation between egg size and care in fishes.

Surprisingly, no study has to date attempted to disentangle the effects of body size, clutch size and egg size on parental care within a multivariate, comparative framework. This is important, as these life history traits are often tightly correlated and traded off against each other (e.g. Smith & Fretwell, 1974; Roff, 1992; Stearns, 1992; Roff, 2002), which may cause effects of single response variables to be either masked or enhanced through inter-correlations. Furthermore, studies should distinguish between pre and post-hatch care, as duration of prehatch care will depend on development time, whereas post-hatch care may be more related to value of the clutch and benefits to offspring. Finally, it is useful to use comparative analyses in order to incorporate shared ancestry between the species or genera (Felsenstein, 1985; Harvey & Pagel, 1991). Since many models on the evolution of both egg size and parental care depend on a strong relationship between life-histories and parental care, it is important to verify the generality of this link using a multivariate comparative approach that controls for as many potential confounding factors as possible.

In order to investigate relationships between body size, clutch size, egg size and duration of care, we compiled a database of quantitative data and assembled phylogenies based on the latest partial phylogenies on the cichlid family of fishes (*Cichlidae*). As cichlid fishes are extremely diverse in all of these life history traits as well as levels of parental care (e.g. Barlow, 1991; Keenleyside, 1991; Goodwin *et al.*, 1998; Barlow, 2000), they are an excellent model taxon to study links

between life histories and care using a multivariate comparative analysis.

Methods

Database

Our database on life histories and duration of care included data for 83–595 species for which we could find information pertaining to any of the key characters of interest: body size (mm total maximum length: 595 species), clutch size (number of eggs in a brood: 247 species), egg size (mm diameter: 236 species) and care duration (days: 83 species). For 25 species we found data on all four key characters. These data originated from Axelrod & Burgess (1988), Brichard (1989), Cichocki (1976), Conkel (1993), Gashagaza (1991), Keenleyside (1991), Kawanabe *et al.* (1997), Konings (1990), Kullander & Nijseen (1989), Linke & Staeck (1994, 1996a, b), Loiselle (1985), Lowe-McConnell (1955, 1959, 1969), Richter (1989), Trewavas *et al.* (1972), Trewavas (1983), Stawikowski & Werner (1998). Most data on egg sizes originated from Coleman (2002) within Fishbase 2002 (Froese & Pauly, 2002). Since species relationships are currently poorly understood below the genus level in cichlids, we could only resolve phylogenetic relationships down to the genus level. Hence, since we had data for all four characters for more than one species in four genera, we treated those species as unresolved polytomies within their genera in the phylogeny. Since a restriction of the analyses to species for which we had data for all four characters created a relatively small sample ($n = 25$), we also used the median of the species values within genera to calculate the genus-level values of each variable. Although this sometimes meant that a value for a character deriving from one species could be matched with a value for another character from another species, it increased our sample size to 33 genera for which we had data for all four characters. This enabled us to further verify the results from the analysis of species-level data. By using care duration as our measure of parental care we could avoid potential intercorrelations between clutch size and other parental care behaviours such as clutch fanning. Our analyses combined bi- and uni-parental species for two reasons. First, there was no significant difference in care duration between bi- and uni-parental genera (ANOVA performed on log-transformed data: $F_{1,36} = 0.001$, $P = 0.97$). Second, addition of the type of care (substrate guarding or mouthbrooding), which often covaries with bi- and uni-parental care, did not affect the results of the analyses. For example, an ANCOVA with care duration as the dependent variable, body size, clutch size and egg size as independent variables and care type as an independent factor showed that there was no significant effect of type of care on care duration ($F_{1,28} = 0.61$, $P = 0.44$).

Phylogeny

To account for the effects of shared ancestry, we assembled a composite tree based on the most recent phylogenies for *Cichlidae* (Fig. 1). The phylogenies used to assemble the tree for the 25 species for which data was available originated from Farias *et al.* (2001), Klett & Meyer (2002), Koblmüller *et al.* (2004) and Salzburger *et al.* (2002). A separate but similar tree, based on the same original phylogenies, was used for the 33 genera for which data originated from genus medians. Farias *et al.* (2001) established the relationship of the genus *Gymnogeophagus* relative to African genera and the Madagascaran genus *Paratilapia*. These data were based on mitochondrial (rRNA 16S and cytochrome *b*), nuclear sequences (Tmo-M27 and Tmo-4C4) and 91 morphological characters from Kullander (1998). The two Tilapiine genera *Boulengerochromis* and *Oreochromis* form an ancestral polytomy relative to all other African genera (Klett & Meyer, 2002). Salzburger *et al.* (2002) established the inter-relationships among six Lake Tanganyikan tribes, Ectodini, Eretmodini, Lamprologini, Limnochromini and Perrisodini and their position relative to the Haplochromine genus *Otopharynx* from Lake Malawi. Salzburger *et al.* (2002) was based on three mitochondrial sequences – 1047 bp of *ND2*, 402 bp of the cytochrome *b* and 974 bp of the control region. The four Lamprologine genera, *Altolamprologus*, *Julidochromis*, *Lepidolamprologus* and *Neolamprologus* form a monophyletic group but relationships between genera are unclear because several genera are polyphyletic (Sturmbauer *et al.*, 1994; Salzburger *et al.*, 2002). Koblmüller *et al.* (2004) established relationships between the seven representatives of the monophyletic tribe Ectodini. Since we could not combine branch length information from different phylogenetic sources, branch lengths were set to be equal to one. This is generally considered to be the most robust and conservative approach when
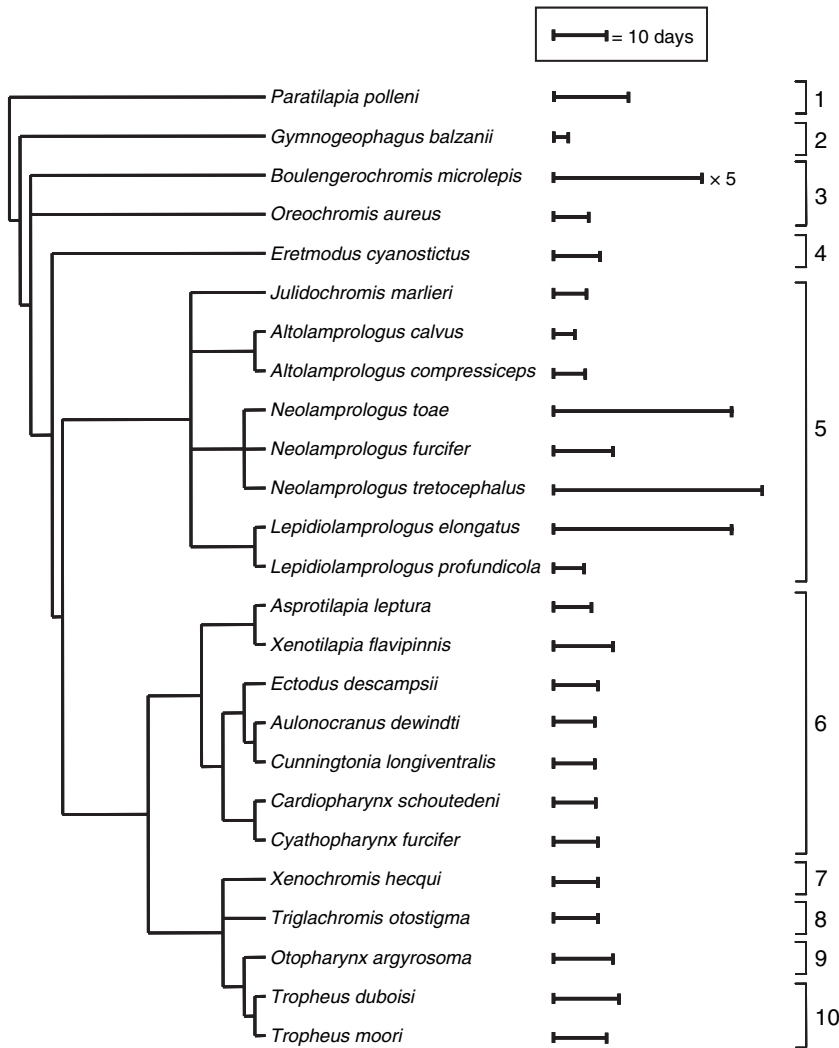

Fig. 1 Phylogeny of the cichlid species included in the study for which we had access to data on body size, clutch size, egg size and care duration. The bars to the right of each species are scaled to the care duration. Numbers to the right of the tree represents the different tribes that the species belong to. Note that *Paratilapia polleni* is not currently placed into any tribe and is therefore only placed into its geographical region of origin: 1, Madagascar; 2, Geophagini; 3, Tilapiini; 4, Eretmodini; 5, Laprologini; 6, Ectodini; 7, Perissodini; 8, Limnochromini; 9, Haplochromini; 10, Tropheini.

actual branch lengths are unknown (e.g. Ackerly, 2000).

Statistical analyses

Bivariate analyses, performed to establish the relationship between all variables, were based on both the raw species values and on the phylogenetically independent contrasts. In the analyses on raw species data, we performed bivariate correlation analyses based on all genera for which we had data on the two variables. This allowed us to maximize the power of each separate analysis but caused sample sizes to differ between analyses. We log-transformed all variables to achieve normality.

The bivariate contrast analyses were performed on the 25 species for which we had data on all variables. The phylogenetically independent contrasts were calculated at all levels in the tree, i.e. between species within genera and between higher nodes. The data are presented graphically by subtracting the smaller value from the larger one for variables shown on the x-axes. The null hypothesis of no relationship between variables would then yield an even distribution of positive and negative values for the variable shown on the y-axis (Felsenstein, 1985; Harvey & Pagel, 1991). This is tested with regressions performed through the origin. Multiple regressions were performed with care duration as the dependent variable and body size, clutch size and egg size as independent variables for independent contrasts derived both from species data and genus data. We also performed a multiple regression with egg size as the dependent variable and clutch size and body size as independent variables for independent contrasts derived from species data since body size has been argued to be an important covariate for this relationship (Elgar, 1990). Also a multiple regression with body size as the dependent variable and clutch size and egg size as independent variables where performed on independent contrasts derived from species data to disentangle the effect of body size on these reproductive traits. Multiple regression analyses on contrast data were also performed through the origin. Independent contrasts were calculated, using the PDAP: PDTREE package of Mesquite (Midford *et al.,* 2002; Maddison & Maddison, 2004), following log-transformation. Polytomies were randomly resolved and assigned zero-length branch lengths. We tested for correlations between the contrasts and their SD to check whether branch length transformations were needed to control type I error rates (Diaz-Uriarte & Garland, 1998). Since the correlations between absolute values of contrasts and their SD were not significant for any of the four characters, no branch length transformations were needed.

All analyses were checked for outliers using sequential removal of all points with residuals more than 2 SD away from the regression line. However, removal of outliers did not change any of the results (i.e. no significant result turned nonsignificant after removal of outliers and *vice versa*) and we therefore present the complete dataset for all analyses. All statistical analyses were performed using Statistica (StatSoft Inc. 2003).

Controlling for effects of hatching time

Since any positive relationship between clutch size or egg size and care duration could be an effect of larger eggs or clutches having longer developmental times, we also checked for correlations between these variables and hatching time. Furthermore, since we used total care duration as our dependent variable, it is important to verify that there is no difference between the effect from life histories on the pre-hatching caring period and the post-hatching caring period. Such a difference could be caused by effects from the actual hatching time of the eggs rather than by parental care decisions based on, for instance, the reproductive value of a brood. We therefore checked whether the pre-hatching care duration was related to total care duration for the genera where we had data on both hatching time and total care duration. Moreover, we replicated the multiple regression analysis performed on raw genera data for total care duration for those genera where we had data on post-hatching care duration. Post-care duration was derived by subtracting time until hatching from total care duration. Due to sample size limitations, we could only perform these analyses on raw genus data.

Results

Analyses based on raw data

Larger bodied species provided longer care (Fig. 2a). Species laying larger clutches showed a nonsignificant tendency to provide longer care (Fig. 2b) but egg size showed no relationship with care duration (Fig. 2c). Egg size was negatively correlated to clutch size (Fig. 2d), and clutch size but not egg size was positively correlated to body size (Fig. 2e, f).

Analyses based on phylogenetically independent contrasts

Bivariate analyses on contrasts showed no relationship between body size and care duration (Fig. 3a). However, clutch size was positively correlated to care duration while egg size was negatively correlated with care duration (Fig. 3b, c). As with the analysis based on raw species data, egg size was again negatively related to clutch size (Fig. 3d) and clutch size, but not egg size, was positively correlated to body size (Fig. 3e, f). The multiple regression analysis agreed with the bivariate analysis in suggesting that there was a negative relationship
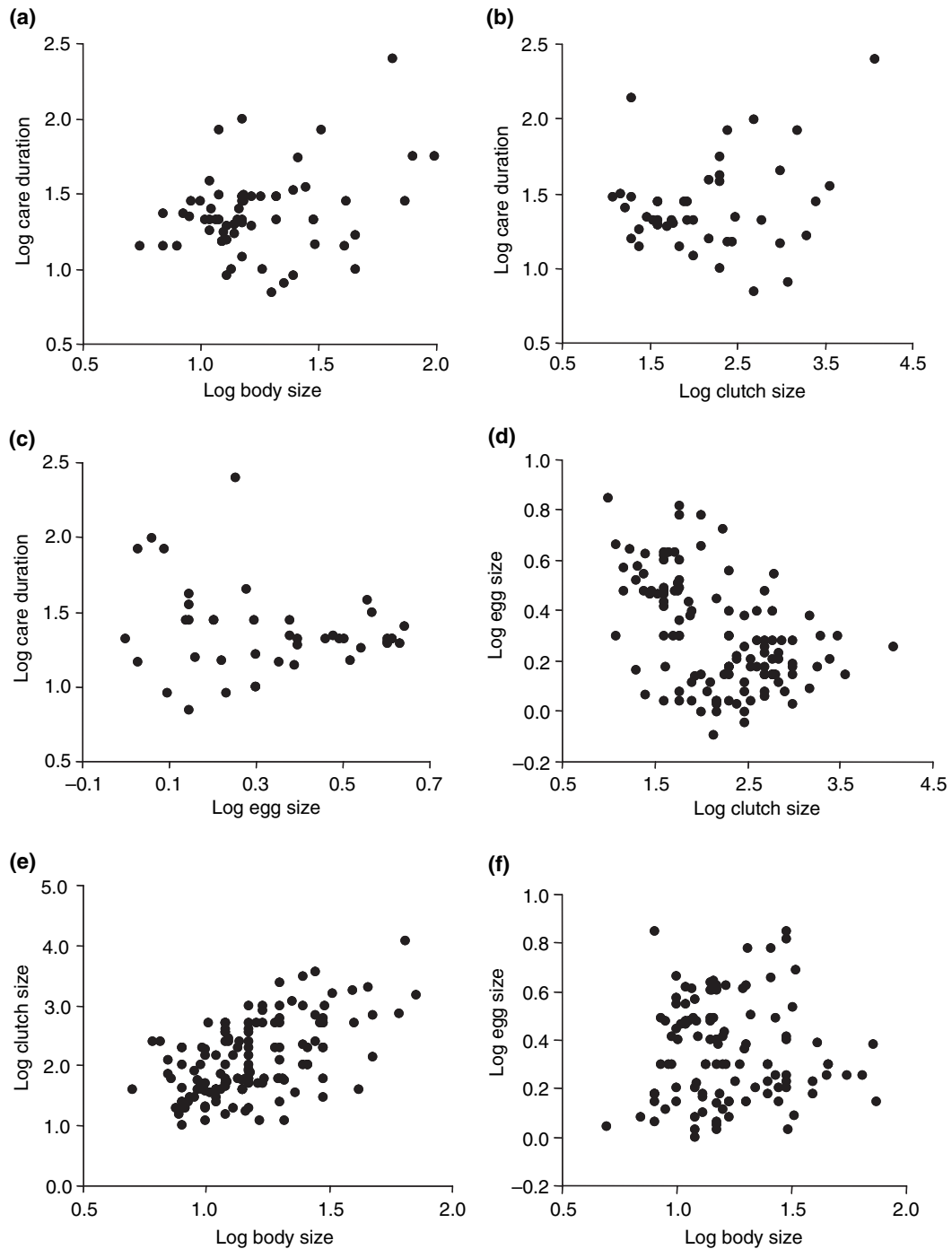
Fig. 2 Bivariate correlations for raw species data. (a) Body size vs. care duration (Pearson correlation: $n = 64$, $r = 30$, $P = 0.02$). (b) Clutch size vs. care duration ($n = 45$, $r = 0.22$, $P = 0.14$). (c) Egg size vs. care duration ($n = 43$, $r = -0.18$, $P = 0.25$). (d) Clutch size vs. egg size ($n = 123$, $r = -0.48$, $P < 0.001$). (e) Body size vs. clutch size ($n = 142$, $r = 0.55$, $P < 0.001$). (f) Body size vs. egg size ($n = 114$, $r = 0.002$, $P = 0.98$).

between the two traits also when controlling for body size (Multiple $r^2 = 0.43$, $F_{2,22} = 8.4$, $P < 0.05$; partial $r = -0.65$, $t_{22} = 4.0$, $P < 0.001$). However, the multiple regression on the relationship between body size and the reproductive traits clutch size and egg size showed that both traits were positively related to body size although the relationship was stronger for clutch size (Multiple $r^2 = 0.59$, $F_{2,22} = 16.0$, $P < 0.0001$; clutch
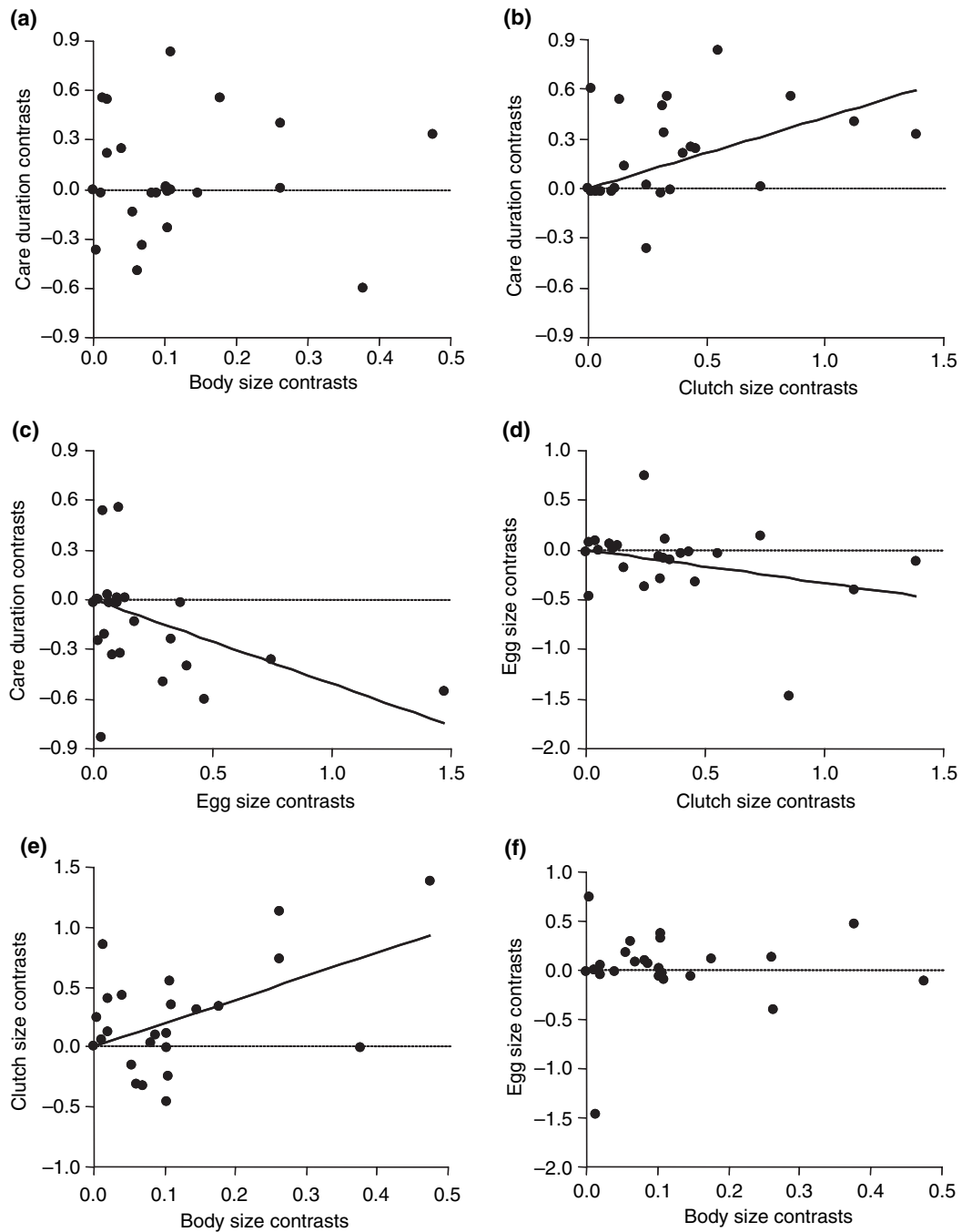
Fig. 3 Results from bivariate regressions, performed through the origin, with the independent variable positivized, for species contrast data. The dashed line represents $y = 0$. (a) Body size vs. care duration ($t_{23} = 0.57$, $r = 0.12$, $P = 0.57$). (b) Clutch size vs. care duration ($t_{23} = 3.8$, $r = 0.62$, $P = 0.001$). (c) Egg size vs. care duration ($t_{23} = 3.2$, $r = -0.56$, $P = 0.004$). (d) Clutch size vs. egg size ($t_{23} = 2.3$, $r = -0.43$, $P = 0.03$). (e) Body size vs. clutch size (linear regression: $t_{23} = 4.1$, $r = 0.65$, $P < 0.001$). (f) Body size vs. egg size ($t_{23} = 0.46$, $r = 0.10$, $P = 0.65$).

size: $\beta = 0.85 \pm 0.15$ SE, $P < 0.0001$; egg size: $\beta = 0.46 \pm 0.15$ SE, $P < 0.01$).

The multiple regressions on the independent contrasts showed a strong relationship between care duration and

clutch size but not between care duration and egg or body size (Table 1). This result was consistent across data deriving from both species and genera (Table 1). Since the tolerance values were high for all independent

Table 1 Results of multiple regressions with care duration as the dependent variable, using species and genus contrast data.

Variable	Species contrasts				Genus contrasts			
	Coefficient	SE	t_{21}	P	Coefficient	SE	t_{29}	P
Clutch size	0.77	0.26	3.0	0.007	0.62	0.23	2.8	0.01
Egg size	−0.19	0.20	1.0	0.34	0.12	0.18	0.7	0.50
Body size	−0.36	0.23	1.6	0.13	0.08	0.21	0.4	0.70

Full model data for multiple regressions: species contrasts, multiple $r^2 = 0.54$, $F_{3,21} = 8.3$, $P = 0.001$; genus contrasts, multiple $r^2 = 0.41$, $F_{3,29} = 6.8$, $P = 0.001$.

variables in the multiple regression model (species contrast analysis: all tolerance values >0.33; genus contrast analysis: all tolerance values >0.32), collinearity was not considered to be a problem (see Quinn & Keough, 2002).

Controlling for effects of hatching time

Prehatching care duration was negatively related to post-hatching care duration ($n = 17$, $r = -0.61$, $P = 0.01$). The analysis on post-hatching care duration supported the results from the multiple regressions on contrast data for total care duration in that clutch size was the main co-variate with care duration (multiple $r^2 = 0.73$, $F_{3,10} = 9.0$, $P < 0.05$; clutch size: $\beta = 0.80$, $P < 0.05$; egg size: $\beta = 0.49$, $P = 0.15$; body size: $\beta = 0.08$, $P = 0.82$). A similar analysis restricted to prehatching care duration found no significant relationships with life history variables (multiple $r^2 = 0.40$, $F_{3,10} = 2.2$, $P = 0.15$; clutch size: $\beta = -0.12$, $P = 0.80$; egg size: $\beta = 0.26$, $P = 0.46$; body size: $\beta = -0.37$, $P = 0.36$). Hatching time was negatively correlated with clutch size ($n = 15$, $r = -0.56$, $P < 0.05$) and positively correlated with egg size ($n = 16$, $r = 0.52$, $P < 0.05$).

Discussion

Our results indicate that clutch size but not egg size or body size is positively linked to care duration in cichlids. Furthermore, our results highlight the importance of investigating the link with life histories using multivariate, comparative methods. The bivariate analyses on raw data suggested that body size and potentially also clutch size co-vary with care duration. However, bivariate and multivariate analyses on independent contrasts showed that only clutch size was positively associated with care duration and hence that it is important to account for shared ancestry when investigating the relationship between care duration and life histories.

The association between clutch size and care duration in this study supports predictions from optimization models of parental care, as well as empirical studies showing that the level of parental effort can be strongly linked to the size of the 'package' of offspring at stake in a given reproductive event (e.g. Gross & Sargent, 1985; Sargent & Gross, 1985,1986; Sargent, 1985; Clutton-Brock, 1991; Roff, 1992; Ackerman & Eadie, 2003). One explanation for this relationship is that an initial increase in clutch size may have driven the evolution of an extended care period as an adaptive response to the increased reproductive value of a larger clutch. Hence, cichlid parents may have shifted the balance of reproductive investment into current reproductive events, which are predicted to be traded off against future survival and reproduction (Clutton-Brock, 1991; Roff, 1992; Stearns, 1992; Sargent, 1997). Our analyses allow us to reject the opposite causation, i.e. that larger clutches have longer developmental times and hence cause a longer duration of care, since we found that larger clutches hatch more quickly. This pattern was probably caused by the fact that larger clutches tended to consist of smaller eggs with shorter hatching times. Since developmental time of eggs generally increases in cool temperatures (e.g. Gillooly *et al.*, 2002), this relationship could also have led to the covariance between clutch size and care duration in our sample if highly fecund species generally spawn in cooler environments. We could not include temperature as a separate variable in our analyses, as these data were not available in the literature for many species. However, again, the negative correlation between hatching time and clutch size rules out temperature differences behind the positive relationship between clutch size and care duration.

Most of our analyses are based on total care duration and hence incorporate both pre and post-hatching care. However, the results of the analyses that distinguishes between these periods of care, although limited in sample size and performed on raw data, suggest that post-hatching care duration is driving the relationships. Interestingly, there was a negative relationship between prehatching and post-hatching care duration. This is likely an effect of egg size on hatching time since hatching time was positively associated with egg size but negatively related to clutch size. This suggests that cichlids have evolved along a continuum between two extremes: (1) large eggs (small clutches) prolonged prehatch and short post-hatch care and (2) small eggs (large clutches), short prehatch and long post-hatch care. Our results therefore show that it is important to distinguish between pre and post-hatching care duration when addressing optimal parental investment.

The strong positive correlation between egg size and care duration reported in other families (e.g. Shine, 1978; Gross & Sargent, 1985; Sargent *et al.*, 1987) was not supported by our bivariate analyses, nor by our phylogentically-based analyses for cichlids. In fact, we did not detect any positive relationship between egg size and care duration even though we detected a strong positive relationship between egg size and hatching time, an effect that one might expect to automatically produce a

positive relationship between egg size and care duration. Instead, our bivariate analysis on contrast data suggests that egg size in fact is negatively correlated to care duration in cichlids. However, this effect, which is likely to be caused by the strong negative relationship between egg size and clutch size evident in this study (also when controlling for body size) disappeared in the multiple regression analysis. Since this is the first study to investigate this phenomenon within a multivariate comparative framework, we cannot yet deduce whether the difference between our results and others is due to genuine taxonomic differences or differences in technique. Since we did not detect any relationship between egg size and care duration even for the bivariate raw data analysis, there may be ecological differences between cichlids and the previously analysed taxa (e.g. centrarchids) in which such a relationship has been reported. One such difference may be the relatively long post-hatching care duration in cichlids (the average post-hatching care duration in cichlids is 26 days (SD = 39.6, $n = 41$)). In species in which a larger proportion of the total care duration is invested into prehatching care, we expect a positive relationship between egg size and care duration due to larger eggs requiring longer developmental times (e.g. Gillooly et al., 2002). However, such a relationship may be considerably weaker for species with relatively long post-hatching care duration (i.e. cichlids). One feature that may lead to a difference in the duration of post-hatching care between cichlids and for instance centrarchids is that several cichlids are socially monogamous (Barlow, 1991). Among monogamous pairs, the male–female association does not break down after the female has spawned her eggs, as it does in most centrarchids (DeWoody & Avise, 2001), and continues during parental care. If the pair bond is maintained across sequential breeding attempts then monogamous individuals avoid the costs associated with searching for a new mate, and they can continue to care for offspring until they are ready to breed again. This could lead to a larger proportion of care being invested into post-hatching care. In contrast, the polygynous centrarchid male must re-nest and court new females, which may create a direct trade-off between his paternal investments in his current brood (i.e. length of time invested in parental care) vs. the likelihood of mating again. This may lead to males only investing in prehatching care and a positive relationship between egg size and care duration due to the longer developmental time of larger eggs. To verify the causes behind the different results in this study compared to previous studies, it would be helpful to re-analyse the link between egg size and care duration within additional families of fishes using the same multivariate comparative approach as we have used for the cichlids.

The lack of covariance between egg size and care duration has implications for several aspects of the theory of the evolution of egg size under parental care. For instance, the 'safe harbour' model of the evolution of parental care (Shine, 1978, 1989), and various extensions of it (e.g. Gross & Sargent, 1985; Sargent et al., 1987) all assume and attempt to explain such a relationship. As these models describe the evolution of increased egg size in response to selection for increased care, they require a link between egg size and care duration. Perhaps direct selection from the environment should be given more prominence in models of the evolution of egg size and parental care.

Another commonly described phenomenon is that egg size increases with female size (e.g. Roff, 1992; Heath & Blouw, 1998). This relationship was evident in the present study also for cichlids, at least when controlling for clutch size. In fishes that provide care this has been suggested to derive from larger females providing the better care required by larger eggs (e.g. van den Berghe & Gross, 1989; Hendry et al., 2001). One particular version of this hypothesis based on that larger eggs require more oxygen and hence more care (or at least a nest that provides higher levels of oxygen) was questioned recently by Einum et al. (2002). Their experimental data suggested that larger eggs did not require more care in the form of increased oxygen levels. Our results suggest that one important measure of parental care (care duration) is not related to maternal size (Table 1) and hence that the positive correlation between egg size and maternal size in fishes cannot simply be explained by larger females providing better care. This fits with Einum et al. (2002) recent suggestion that other factors (e.g. density dependence or food abundance) must lie behind this relationship.

To conclude, our study investigates, for the first time, how body size, clutch size and egg size are related to care duration using multivariate analyses that account for phylogenetic relationships. We suggest that instead of coevolving with egg size, parental care in this family may have evolved as a response to the value of a clutch, driven primarily by clutch size. Furthermore, relationships appear to be driven by post-hatch care rather than pre-hatch care. The next step towards explaining the evolution of parental care in fishes in relation to life histories will be to use temporal analyses to reconstruct evolutionary shifts in clutch size in relation to changes in care duration and other life history and ecological traits. Comparative studies on other families accounting for both the effects of covariates as well as phylogeny are required to test the generality of our findings in Cichlidae. In the meantime, models on the evolution of parental care in fishes may benefit from incorporating clutch size to a stronger degree.

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