The evolution of gregariousness in parasitoid wasps

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Data are assembled on the clutch-size strategies adopted by extant species of parasitoid wasp. These data are used to reconstruct the history of clutch-size evolution in the group using a series of plausible evolutionary assumptions. Extant families are either entirely solitary, both solitary and gregarious, or else clutch size is unknown. Parsimony analysis suggests that the ancestors of most families were solitary, a result which is robust to different phylogenetic relationships and likely data inadequacies. This implies that solitariness was ubiquitous throughout the initial radiation of the group, and that transitions to gregariousness have subsequently occurred a minimum of 43 times in several, but not all lineages. Current data suggest that species-rich and small-bodied lineages are more likely to have evolved gregariousness, and contain more species with small gregarious brood sizes. I discuss the implications of these data for clutch-size theory.

Keywords: clutch size; parasitoid; Hymenoptera; evolution; life histories; gregariousness

1. INTRODUCTION

The evolution of clutch size is one of the oldest and most enduring topics in behavioural ecology and life history theory (Roff 1992; Stearns 1992). Two different theoretical approaches have been taken towards this topic (Godfray 1987a; Godfray *et al.* 1991). The first, and oldest, considers the decision only from the perspective of a mother, and asks how different circumstances may affect the clutch size which maximizes her fitness (Wilson & Lessells 1994). A second approach considers not just the mother's perspective but also that of her offspring. The clutch size which maximizes the fitness of offspring is frequently less than that of parents, because parents are normally equally related to all offspring in a brood, whereas offspring have to compete with siblings which only share some of their own genes (Godfray 1995). Thus, there is potentially widespread parent–offspring conflict over clutch size, and the solution of this conflict may produce clutch sizes which differ from those predicted by traditional models (see, for example, Parker & Mock 1987).

The latter approach to clutch size has particular relevance to parasitoid wasps (Hymenoptera). Parasitoid wasps are a species-rich group of organisms which lay their eggs on or in the bodies of other insects (Quicke 1997). The larvae feed on the still-living body of the host, eventually killing it. Parasitoid wasps show a great diversity of life history parameters, including clutch size, which has made them the subject of a large programme of research in recent years (Godfray 1994). For example, many parasitoid species are 'solitary', meaning that only one offspring is ever produced per host. Others are 'gregarious', where several offspring may be reared from a single host. Models of parent–offspring conflict have shown that the brood size which maximizes a parent's

fitness is frequently not achievable because under a range of circumstances it pays siblings to kill each other to control the entire host (Godfray 1987b; Rosenheim 1993). One such circumstance is when broods comprise a small multiple-egg clutch, such as two or three eggs. As a result, small gregarious broods are predicted to be less evolutionarily stable than other brood sizes. This may sometimes prevent the evolution of small gregarious broods as well as transitions from solitary to gregarious states. One empirical study (le Masurier 1987) appears to support this prediction.

Three facts would help ascertain the power of models such as these in parasitoid wasps: first, a thorough knowledge of the clutch sizes shown in extant taxa; second, the clutch sizes of the ancestors of modern parasitoids, and the evolutionary changes in brood size which have occurred; and third, the ecological correlates of the evolution of gregariousness. Such facts form the empirical framework on which models of clutch-size evolution must hang.

Data on clutch size have never been assembled for all the families of parasitic wasps. In addition, until recently there was very little consideration of the phylogenetic relations between parasitic wasps (Quicke 1997). Not surprisingly, therefore, an analysis of likely ancestral states and ecological correlates across the whole group has never been done. Rosenheim (1993) assembled data for several families from a number of studies. He showed that several families only contained solitary species, whereas others contained both solitary and gregarious species. This implies that solitariness is ancestral and that gregariousness may have evolved a number of times in different taxa. Several studies have addressed ecological correlates of clutch size within families, genera, or species (see Godfray 1994), but never across the entire group.

Here I build on these leads. I assemble the existing clutch-size data for all families of parasitic wasp, including a survey of species with small gregarious broods. I use these data to reconstruct the evolution of clutch size in the group from recent phylogenetic research. I investigate species richness and body size as correlates of clutch-size evolution. Finally, I discuss the implications of these data for the theory of clutch-size evolution in parasitic wasps.

2. METHODS

(a) *States of extant taxa*

A species-level survey of clutch size in the parasitoid Hymenoptera is presently impractical and would have limited use. There are 65 families which might be included in such a survey, and to assemble a species-level data set from published life history data would take many years while leaving considerable biases and gaps at generic or higher taxonomic levels. There are also very few estimates of phylogeny within families, considerably hampering interpretation of the data at this level. Instead, I restricted my survey largely to the family level, because most families have received both some phylogenetic and life history treatment (table 1). The data were checked and updated in consultation with expert taxonomists (see acknowledgements). The data were also checked against a large species-level data set which included clutch-size information (Blackburn 1990), and against the data on small gregarious brood sizes described below. For taxonomic treatment of families I followed Gauld & Bolton (1988). It was not obvious whether to include certain families in the analysis because they contain a large proportion of non-parasitoid species. I made the following decisions on inclusion: the only (parasitoid) symphytan family included was the Orussidae. In the aculeates I excluded the Apidae, Formicidae, Vespidae, and Sapygidae because they are not parasitic, but I included other non-social nest-building families because the relevant biology approximates to that of other parasitoids (see Godfray 1994). Of the Parasitica, I only excluded the Agaonidae and Cynipidae as being largely phytophagous. I classified each family as either lacking clutch-size data, containing solitary species, gregarious species, or both, insofar as is shown by current data. A dichotomous (solitary–gregarious) classification was used because this is the most common way in which brood-size data are presented in the literature. Where texts gave different opinions on brood size range, I used the estimate giving the broadest range.

I made more detailed coverage of brood size in two ways. First, some families are especially species-rich and have received detailed taxonomic and biological treatment at the subfamily level. I therefore refined the analysis to include subfamilies where possible, specifically in the Eulophidae, Braconidae, and Ichneumonidae.

Second, I was interested in obtaining information about a particular type of brood size; multiple egg clutches with only a few eggs. Such clutches are interesting because models of parent–offspring conflict suggest they should be rare. Knowing the distribution of such brood sizes is thus a step towards testing the relevance of this particular theoretical approach, and how its applicability may vary between taxa (Rosenheim 1993; Mayhew & Hardy 1998). A species-level survey is required for this. I therefore made a directed search of the clutch-size literature. I recorded any parasitic wasp species where clutch size was on average greater than 1.5 and less than or equal to 4, but I ignored species where only one offspring per host normally survives. I chose 1.5 as the lower limit to prevent

inclusion of many solitary species which sometimes lay more than one egg. However, this lower limit will also exclude some facultatively solitary species which only occasionally lay in large hosts. I chose 4 as a typical maximum brood size where a gene for siblicide can invade the population in the parameter space of theoretical models (see Godfray 1987*b*; Rosenheim 1993), although the critical brood size can vary with different biological assumptions. As on-line literature searches and systematic use of abstracts were not effective at locating the relevant information, I used a less repeatable search method, of first using large reviews or comparative studies on clutch size (Clausen 1940; Iwata 1976; Clausen 1977; Blackburn 1990; Ridley 1993; Godfray 1994), and then following leads given in citations. The decision to terminate the search was taken subjectively on diminishing returns. The raw data and list of references are available on request from the author.

I hypothesized that species-rich and smaller-bodied taxa were more likely to evolve gregariousness: species-rich taxa may have evolved faster or possess more diverse biologies which enable gregariousness to evolve. Small bodies may 'preadapt' a lineage for gregariousness by reducing offspring resource limitation. To investigate the effect of species richness and body size I mainly used the data in Brown (1982). To control for phylogeny when investigating these effects I used phylogenetic regression (PR) (Grafen 1989) on a composite 'best-estimate' of phylogeny following Dowton & Austin (1994), Brothers & Carpenter (1993) and Ronquist (1995). Current comparative methods suffer from a number of inadequacies when applied to both categorical (Ridley & Grafen 1996) and continuous variables (Price 1997), and PR is used here as one of the better performing, if imperfect, available applications (Purvis *et al.* 1994; Grafen & Ridley 1996).

Known family species richness varies by over four orders of magnitude, so it is probably a robust relative measure of true species richness, because bias in knowledge between groups would have to vary over similar magnitudes to account for these differences. However, biases in knowledge of different families could have important effects on both the known clutch-size range, and the number of species surveyed with small gregarious brood sizes, and it would therefore be important to control for potential study bias in any analysis of these variables. One way to measure study bias is to observe how often families are mentioned in the literature relative to that expected from their species richness. As a measure of the amount of study done on each family, I scored the frequency ('hits') with which each family was mentioned in the Life Sciences Collection published by Cambridge Scientific Abstracts 1982–1995. In a phylogenetic regression, the frequency with which a family is mentioned in the literature is highly correlated with its known species richness ($\ln[\text{hits}+1] = 0.5769$. $\ln[\text{species}]$, $F_{(1,27)} = 78.01$, $p < 0.0001$). I calculated the residual *y*-values when this regression equation is fitted to the species richness data for each family, and included these residuals in each analysis as a control for study bias.

(b) *Reconstructing ancestral states*

As brood size is not a character which fossilizes, ancestral states have to be inferred from what is known from the states of extant taxa. Thus, estimates need to be made of phylogenetic relatedness. There is little consensus on phylogenetic relations for most parasitoid Hymenoptera (Gauld & Bolton 1988; Quicke 1997). Therefore, I explored a range of phylogenetic hypotheses, and did a separate analysis on each of them. Specifically, I varied the interfamily relationships according to the

Table 1. *Clutch size, species richness, body size and amount of research on the families of parasitoid wasps*

superfamily	family	clutch size: solitary (s), gregarious (g), unknown (?)	species with clutch size $\geqslant 1.5$, $\leqslant 4$ (this study)	species described ([h]except where stated)	body length, mm ([h] except where stated)	hits in Cambridge Life Sciences Collection, 1982–1995
Orussoidea	Orussidae	s[a]	0	75	5–20	13
Stephanoidea	Stephanidae	s[b]	0	100	4–40	9
Trigonalyoidea	Trigonalyidae	s[a]	0	100	8–17	5
Megalyroidea	Megalyridae	s[c]	0	175	4–20	5
Ceraphronoidea	Megaspilidae	s+g[d]	0	250	1–5	21
	Ceraphronidae	s+g[d,e]	1	150	0.5–5	13
Evanioidea	Gasteruptidae	s[a]	0	500	<28	0
	Aulacidae	s+g[a,f,g]	0	250	1–20	15
	Evaniidae	s[a]	0	500	2–15	11
Cynipoidea	Figitidae	s[a]	0	250	1.5–5	8
	Liopteridae	?[h]	0	65	4–15	0
	Charipidae	s[i]	0	150	<2	4
	Ibaliidae	s[a]	0	15	8–25	4
	Eucoilidae	s[f]	0	700	0.75–5	80
Proctotrupoidea	Austroniidae	?[h]	0	3	6	1
	Peradeniidae	?[j]	0	2[j]	no data	2
	Vanhorniidae	?[h]	0	1	6	1
	Proctotrupidae	s+g[a,h]	1	300	6–8	8
	Pelecinidae	s[a]	0	1	30–60	4
	Roproniidae	?[h]	0	8	8–10	4
	Monomachidae	?[h]	0	13	7–22	2
	Diapriidae	s+g[a]	0	1200	3–15	39
	Heloridae	s[h]	0	9	7	9
	Platygasteridae	s+g[a]	0	987[o]	0.5–5	17
	Scelionidae	s+g[i]	1	2768[o]	0.5–15	209
Chalcidoidea	Mymarommatidae	?[k,l]	0	9[i]	<0.7 (forewing)[i]	6
	Eurytomidae	s+g[a]	0	1100	3–5	126
	Encyrtidae	s+g[a]	4	2800	0.5–5	87
	Pteromalidae	s+g[i]	5	2800	1–4	14
	Trichogrammatidae	s+g[a]	12	440	0.5–1	347
	Mymaridae	s+g[a]	5	1200	0.2–2	119
	Chalcididae	s+g[a]	0	1400	2–12	138
	Eucharitidae	s[a]	0	330	3–10	15
	Eupelmidae	s+g[a]	0	700	1–8	58
	Torymidae	s+g[i]	1	1000	1–6	87
	Elasmidae	s+g[i]	1	220	1–3	14
	Aphelinidae	s+g[f]	5	800	0.35–2.5	347
	Signiphoridae	s+g[i]	0	75	0.5–1	7
	Tanaostigmatidae	?[h]	0	33	2–3	6
	Leucospidae	s[a]	0	123	2–16	6
	Eulophidae	4 subfamilies, 4 s+g[l]	19	3000	<5	437
	Rotoitidae	?[k]	0	1[k]	0.8[k]	1
	Perilampidae	s[a]	0	200	1.5–7	17
	Ormyridae	s[k]	0	50	1.5–3	8
	Tetracampidae	s+g[k,l]	0	35	0.8–3.3[i]	4
Vespoidea	Tiphiidae	s[i]	0	1500	4–30	40
	Mutillidae	s[f, i]	0	5000	3–30	54
	Bradynobaenidae	?[h]	0	200	3–20	1
	Pompilidae	s[h]	0	3000	3–60	94
	Scoliidae	s[h]	0	300	8–60	29
	Rhopalosomatidae	s[f]	0	25	2.5–20	1
	Sierolomorphidae	?[h]	0	10	3.5–6	2
	Masaridae	s[h]	0	230	no data	9
	Eumenidae	s[h]	0	3000	no data	85
Apoidea	Sphecidae	s[i]	0	7700	2–50	457
Chrysidoidea	Scolebythidae	?[h]	0	3	no data	3
	Sclerogibbidae	s+g[a]	1	20	3–7	6

continued

Table 1   *(continued)*

superfamily	family	clutch size: solitary (s), gregarious (g), unknown (?)	species with clutch size $\geqslant 1.5$, $\leqslant 4$ (this study)	species described ([h]except where stated)	body length, mm ([h] except where stated)	hits in Cambridge Life Sciences Collection, 1982–1995
	Embolemidae	?[h]	0	12	1.3–5	7
	Dryinidae	s+g[f]	0	850[o]	1.5–10	63
	Chrysididae	s+g[d]	1	3000[o]	2.5–20	75
	Bethylidae	s+g[i]	18	2000[o]	1–10	89
	Plumaridae	?[h]	0	20	3–10	0
	Loboscelidiidae	?[h]	0	20	2–5	0
Ichneumonoidea	Ichneumonidae	34 subfamilies, 24 s, 7s+g, 3 ?[m]	0	15 000	2–40	840
	Braconidae	46 subfamilies, 24 s, 4g, 9 s+g, 9 ?[n]	12	10 000[o]	2–15	1453
13	65	24 s, 26 s+g, 15?	87	76 778	—	6535

[a]Iwata (1976), [b]Taylor (1967), [c]Rodd (1951), [d]Rosenheim (1993), [e]Moutia & Courtois (1913), [f]Clausen (1940), [g]Deyrup (1984), [h]Brown (1982), [i]Gauld & Bolton (1988), [j]Naumann & Masner (1985), [k]J. Noyes (personal communication), [l]J. LaSalle (personal communication), [m]I. Gauld (personal communication), [n]C. van Achterberg (personal communication), [o]Godfray (1994).

molecular analysis of Dowton & Austin (1994), and the largely morphologically based opinions of Königsmann (1978), Rasnitsyn (1988), and Whitfield (1992). For lower-order relationships I used the strict consensus tree of Quicke & van Achterberg (1990, their figs 1 and 2*f*) for braconids, the composite cladogram of Brothers & Carpenter (1993, their fig. 11) for aculeates, and the most parsimonious tree of Ronquist (1995, his fig. 18) for cynipoids. Taxa which were not represented in the cladograms were excluded from the analysis. Taxa which received treatment only at higher levels were clustered in soft polytomies (nodes representing unknown relationships between more than two daughter clades). I also investigated a purely taxonomic hypothesis using hierarchical soft-polytomous clustering of subfamilies, families, superfamilies, infraorders and finally suborders.

Analysis was done in the MacClade computer package (v. 3.0, Maddison & Maddison 1992). MacClade reconstructs ancestral states of unordered categorical characters using Fitch parsimony (Fitch 1971). The parsimony algorithm distils information from all parts of the tree surrounding any node by taking as its solution those states occurring in the greatest number of three sets of most parsimonious solutions for a node; those from the left and right descendents, and that from the ancestor. Consistency (CI) and character retention indices (RI) were calculated (Farris 1989) for each reconstruction. The CI measures how close the number of reconstructed character steps is to the minimum possible on any tree (as a proportion where 0 = infinitely more, 1 = minimum). The RI measures whether the observed number of steps reconstucted on the tree in question is closer to the minimum or maximum possible on any tree (as a proportion where 0 = maximum, 1 = minimum).

The following reservations about the analysis should be noted: first, whether clutch size is classified as continuous or discrete affects the calculation of ancestral states. The relevance of the dichotomous classification rests on the assumption that transitions from brood sizes of one to two are qualitatively different from transitions between any other brood size. The generality of this assumption is unknown. Second, the data on brood size are potentially erroneous because they derive from multiple sources and some taxa are very poorly surveyed.

Addition of more data could potentially change the outcome of the analysis. Third, the reconstruction of ancestral states assumes a specific parsimonious model of evolution. The relevance of this model for parasitoid clutch size is unknown. Finally, the true phylogenetic relations between extant taxa are unknown, and may affect the outcome of the analysis. The conclusions of the analysis might reasonably be rejected for any of the above reasons. However, the problems of uncertain taxonomy and of uncertain data can be circumvented to some extent by exploring a range of phylogenetic hypotheses and possible character states, which MacClade easily allows. The assumption of dichotomous clutch size and the evolutionary model remain plausible but unproven.

3. RESULTS

(a) *Extant brood sizes*

A total of 146 terminal taxa were included in the analysis. Of the 65 families, 24 only are known to contain solitary species, none contain only gregarious species, 26 are known to contain both solitary and gregarious species, and no clutch-size information exists for 15 families (see table 1). In the family Ichneumonidae, 24 subfamilies are only known to contain solitary species, seven are polymorphic, and clutch size is unknown for three. In the Braconidae, 24 subfamilies are solitary, four are gregarious, nine are polymorphic, and in nine clutch size is unknown. All four eulophid subfamilies are polymorphic for clutch size. In total, 72 terminal taxa are solitary, four are gregarious, 43 are polymorphic and no data exist for 27 (table 1). I also assembled data on 87 species with small gregarious broods in 15 of the 26 families with gregarious species (table 1).

In a multiple PR, ln[species richness] had a significant positive effect on whether clutch size was known or unknown; ln[body length] and residual ln[hits+1] had no significant effects (table 2). Both smaller body size and higher species richness significantly increased the probability of gregariousness being present in a lineage (see

Table 2. *Results of multiple phylogenetic regressions*

(*F* ratios for each independent variable are calculated after controlling for other independent variables. Denominator degrees of freedom reflect the number of independent contrasts on the phylogenetic tree.)

dependent variable	independent variable	slope	*F*	d.f.	*p*
clutch size known (2) or unknown (1)	residual ln[literature hits+1]	0.043	1.056	1,22	> 0.1
	ln[species richness]	0.104	22.87	1,22	< 0.001
	ln[body length, mm]	0.031	0.526	1,22	> 0.1
gregarious clutches known (2) or unknown (1)	residual ln[literature hits+1]	0.063	2.01	1,22	> 0.1
	ln[species richness]	0.121	19.76	1,22	< 0.001
	ln[body length, mm]	−0.139	4.53	1,22	< 0.05
species with small gregarious broods (ln[*n*+1])	residual ln[literature hits+1]	0.226	7.47	1,22	< 0.05
	ln[species richness]	0.149	11.51	1,22	< 0.01
	ln[body length, mm]	−0.262	6.86	1,22	< 0.05

table 2). The number of species recorded with small gregarious broods (ln[*n*+1]) was significantly higher in more completely studied taxa, significantly higher in species-rich taxa, and significantly higher in smaller taxa (table 2). Contrasts with large residuals included the Bethylidae versus the Chrysididae, the contrast between the chalcidoid families, and the Braconidae versus the Ichneumonidae. This makes intuitive sense as the Bethylidae, Trichogrammatidae, Eulophidae, and Braconidae displayed high numbers of such species, whereas the Ichneumonidae displayed low numbers of such species.

(b) *Transitions in brood-size strategy*

The tree based on Dowton & Austin (1994) returned 43 unambiguous transitions between solitary and gregarious states and zero unambiguous transitions between gregarious and solitary states as the most parsimonious result (tree length 45+). The consistency index was high (CI = 0.96), and the retention index moderate (RI = 0.33). The result was identical when the ancestral branch was fixed as gregarious. When the analysis was repeated with all poorly researched solitary families (less than 20 literature hits) assumed to be polymorphic, the only difference was a corresponding increase in the number of transitions from solitariness to gregariousness (55).

Results were identical under the phylogenetic hypotheses of Rasnitsyn, Königsmann, and Whitfield. In the taxonomic clustering the most parsimonious solution returned only 33 unambiguous transitions. When soft polytomies across the whole taxonomic tree were resolved into random bifurcations 250 times, the number of solitary to gregarious transitions in the random trees ranged from 37 to 46 with a mean of 43.56. Some trees also returned a few gregarious to solitary transitions: ranging from 0 to 3 with a mean of 0.06. Consistency indices ranged from 0.93 to 0.96 with a mean of 0.94. Retention indices ranged from 0 to 0.33 with a mean of 0.08. Thus, results were very similar to those based on cladistic estimates of phylogeny, and the estimated number of evolutionary transitions seems very robust to uncertainties in extant character states and different phylogenetic hypotheses.

4. DISCUSSION

With the reservations noted in § 2, the data in this paper suggest the following points.

1. That extant families are entirely solitary, or contain both solitary and gregarious species, or are unknown with respect to clutch size.
2. That both species-rich and small-bodied taxa are more likely to contain gregarious species and species with small gregarious broods.
3. That the solitary state is ancestral to nearly every family in the parasitic Hymenoptera, and therefore that it was largely retained through the early diversification of the group.
4. That gregariousness then evolved at least 43 times independently in at least 26 of the 65 families.

The most important of the above results is that gregariousness has evolved many times in parasitoids from a solitary ancestral state. This confirms Rosenheim's (1993) suggestion that the stringent conditions for the evolution of gregariousness advocated by Godfray (1987*b*) must frequently be relaxed. At present it is unknown if the evolution of gregariousness has been accompanied by the changes in larval behaviour suggested by Godfray (1987*b*), or if only adult oviposition behaviour has changed. Comparative studies of larval behaviour versus clutch size might be able to distinguish these two possibilities. The last review of parasitoid larval competition (Salt 1961) identified brood reduction behaviour in several families, and this data set could probably now be considerably enlarged.

A second important result is that many species develop in small gregarious broods, suggesting that such brood sizes may sometimes be evolutionarily stable, especially in the Bethylidae, Trichogrammatidae and Eulophidae. All these families have received some previous attention as exceptions to the dichotomy advocated by Godfray (1987*b*): trichogrammatids are egg parasitoids which may need to consume the entire host to develop successfully, and in a large egg several individuals are needed (Godfray 1987*b*). Bethylids, for which the clutch-size distribution is well documented (Mayhew & Hardy

1998), have a biology which gives high within-brood relatedness. The same is true for some eulophids, which have single-sexed broods, enhancing the genetic costs of siblicide (Rosenheim 1993). Thus, three different mechanisms for the stability of non-siblicidal behaviour have been invoked in three different taxa. If such biologies could arise in previously solitary species, they would also provide a potential mechanism for the evolution of gregariousness from siblicidal solitary species.

A third important result is that species richness and body size are causes or effects of the evolution of gregariousness. It seems unlikely that gregariousness is a main cause of species richness because most parasitoid species remain solitary (Mayhew & Hardy 1998). However, it is very plausible that gregariousness would more likely evolve in species-rich taxa: such taxa would obtain more 'tickets in the evolutionary lottery' (Williams 1975), perhaps from greater biological diversity or from a longer evolutionary history. Body size could plausibly be both a cause and effect of clutch-size evolution, because body size and clutch size are often traded-off in parasitoids (Mayhew 1998). Larger bodied species on hosts of given size are more likely to be resource-limited, and hence solitary, but solitary species on hosts of given size are more likely to have larger bodies. How these results are interpreted therefore depends on a knowledge of how host size has evolved alongside body size and clutch size.

In conclusion, this study suggests several avenues of comparative research which might contribute towards evolutionary theory of clutch size in parasitoids, and in particular which might help distinguish between the appropriateness of different theoretical approaches. The data presented here suggest that siblicidal behaviour among parasitoid larvae cannot always be a constraining influence on clutch-size evolution, and it remains to be seen whether the transitions to gregariousness and apparent stability of small gregarious broods in some taxa can be explained within the current framework of parent–offspring conflict models. Finally, the results presented here should be confirmed by improved comparative methods and by new data on clutch size, phylogenetic relationships, and the process of clutch-size evolution.

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