RESEARCH ARTICLE

Maternal Care, Iteroparity and the Evolution of Social Behavior: A Critique of the Semelparity Hypothesis

Stephen T. Trumbo

Abstract The Semelparity Hypothesis (Tallamy and Brown in Animal Behav 57:727–730, 1999) predicts that among insects with parental care that iteroparity will be rare. It represents two important challenges. First, life history ecologists have sometimes linked extended parental care with iteroparity, not semelparity, as part of a suite of correlated characters associated with K-selective environments. Second, behavioral ecologists have developed theories for the evolution of eusociality that rely upon a subsocial species producing multiple cohorts of offspring, a precondition for offspring allocare and/or inheritance of a social unit. Using a database of invertebrates exhibiting maternal care in Costa (The other insect societies. Harvard University Press, Cambridge, 2006), the association between semelparity and maternal care was tested using a broad comparative analysis. Semelparity was found in only 24.5 % of the best-studied representative species. In addition, semelparity was more rare in species that form nests, burrows or galleries (12.1 %) than in species that guard offspring out in the open (45.0 %). Iteroparity was common both among nesting species with non-overlapping broods (serial nesting) and in species where a female produces broods of different aged offspring in the same nest (within-nest iteroparity). It is hypothesized that common factors, particularly rapid juvenile development on high quality resources, facilitated both serial nesting and parental care. Within-nest iteroparity is an essential stage in the evolution of eusociality that has often been overlooked. Recent models of sibling conflict and reproductive spacing suggest that parental care can be an indirect cause of within-nest iteroparity despite the fact that parental investment can lead directly to diminished future reproduction. The reversal of this life history correlation may occur as a result of the transition between asocial and subsocial nesting behavior; analogous reversals may be a frequent outcome of transitions between levels of social organization.

Keywords Sibling conflict · Social evolution · Kin selection · Viviparity · Brood care · Cooperative breeding · Parity

Introduction

The female dung roller, *Kheper nigroaeneus*, can spend 3 months caring for a single offspring: preparing a large brood ball, reducing fungal contamination, re-coating with excrement and soil after the larva and parent have fed, and preventing desiccation (Edwards 1988; Edwards and Aschenborn 1989). A successful female will produce but one or two young per year for several years, a reproductive rate comparable to many of the mammal species that provide her food. Her care will ensure a high probability that each offspring will survive the juvenile period (58–84 %). While *K. nigroaeneus* is a serial nester, other care-givers like the passalid beetle, *Odontotaenius disjunctus*, produce multiple broods within a single long-lasting nest (within-nest iteroparity) (Schuster and Schuster 1985). Separate cohorts of offspring in the same nest permit the evolution of allocare; adult offspring of *O. disjunctus* work alongside their parents to repair and maintain pupal cells for their younger siblings (Schuster and Schuster 1997).

These examples challenge the Semelparity Hypothesis, according to which maternal care in insects is predominantly

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associated with semelparity (Tallamy and Brown 1999; Tallamy 2000, 2005). Semelparity (one reproductive bout per lifetime per female) and iteroparity (multiple reproductive bouts per female) are descriptors introduced by Cole (1954) and adapted by Fritz et al. (1982) for insects, many of which have short breeding cycles and a generation time of less than a year. Maternal care is used in the present paper to refer to extended care or subsocial behavior, that is, care beyond resources placed into eggs and the selection of an oviposition site. Tallamy and Brown's (1999) argument is twofold. (1) Most care-giving insects are hypothesized to have evolved from species that were ecologically or phylogenetically constrained to semelparity. The uncertainty of a second reproductive attempt (whether from a scarcity of opportunity or from extrinsic mortality) selects for maximal care for the initial brood, sometimes in spite of only modest benefits from care. More recently, Klug and Bonsall (2009) have modeled how high adult mortality rates can favor care of eggs even when the benefits of care are limited. (2) Selection for increased parental investment, in turn, reduces resources for the maintenance of the soma and for future reproduction (Williams 1966; Trivers 1972). There are, indeed, numerous examples of experimentally induced increases in parental investment leading to future reproductive costs: a decrease in longevity (Creighton et al. 2009), a decrease in future fecundity (Tallamy and Denno 1982; Fink 1986; Olmstead and Wood 1990; Zink 2003), and an increase in the inter-clutch interval (Bosch and Slattery 1999; Agrawal et al. 2005). Similar insight into tradeoffs between parental investment and future reproduction can be seen by comparing closely related species that differ in levels of parental care (Kaitala and Mappes 1997). Clearly, parental investment can decrease the probability of future reproduction. Stegmann and Linsenmair (2002) call this the 'weaker claim of the semelparity hypothesis', that in comparisons within species or among closely related species, iteroparous females tend to provide less care than semelparous females. But just how tightly coupled is parental care to semelparity among insects, and does the transition from asocial to particular forms of subsocial behavior open up indirect routes allowing iteroparity to emerge or re-emerge after the initial decrement to female survival and fecundity? Transitions to new levels of social organization (single cell to multicellular, solitary to eusociality) initiate complex interactions and feedbacks among life history variables that can produce non-intuitive outcomes (Maynard Smith and Szathmáry 1995; Bourke 2011). Stable suites of traits cannot always be predicted by analysis of the directional effect of changing a single variable (Van Dyken and Wade 2012b).

There has been no broad evaluation of the Semelparity Hypothesis even though it represents a major shift in perspective. Prior to Tallamy and Brown (1999), many life history ecologists thought of iteroparity and parental care

as a positive rather than a negative association (Southwood 1977; Begon and Mortimer 1981; and more recently Vandermeer and Goldberg 2003) with iteroparity and parental care included among a suite of K-selected, equilibrial or homeostatic traits. Among insects, stable and structured (K-selecting) environments were thought to favor parental care (Wilson 1975). Presentations of life history trait extremes, however, vary considerably. Ricklefs (2008) and Price et al. (2011) include parental care, but not iteroparity, as a trait of organisms with a 'slow' or K life history. Other authors continue to reproduce the original compilation of traits of Pianka (1970) (see Fotelli 2001) that includes iteroparity as a K-selected trait without mention of parental care. Parental care and semelparity, however, have never been linked generally by life history ecologists in such compilations of traits for species with determinate growth.[1] Such an association would require a rethinking of life history formulations for invertebrates.

A parental care-semelparity association also presents a formidable problem for theories of the evolution of eusociality. Current models of the origin of eusociality agree that important preconditions were subsocial behavior, a defensible nest, provisioning of food, and the delayed dispersal of offspring that could be selected to care for younger siblings (Queller and Strassman 1998; Linksvayer and Wade 2005; Korb 2007; Wilson 2008; Nowak et al. 2010). No hypotheses have been proffered, however, of why subsocial females should produce two broods of young before allocare or delayed dispersal evolved. While few students of eusociality have addressed this semelparity barrier, Alexander et al. (1991, p. 30) considered and accepted it, and suggested that the preponderance of semelparity among subsocial insects might explain why even more nesting species did not give rise to eusocial descendants. Here, it is argued that iteroparity is the predominant pattern for subsocial insects. The association is especially strong for subsocial species that nest, occurring as serial nesting with non-overlapping broods or as within-nest iteroparity with different-aged offspring in the same nest. Serial nesting may be best explained by life history and ecological factors that selected for both iteroparity and parental care. For within-nest iteroparity, on the other hand, selection on the mother to reduce sibling competition can be an indirect cause of iteroparity. Such selection would have to more than offset the direct effect of parental investment on reducing future reproductive potential. Plausible mechanisms for the evolution of within-nest iteroparity can be constructed by combining insights from

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[1] In groups with indeterminate growth where increasing body size is positively correlated with fecundity, iteroparity has been linked to a large body size and a lack of parental care, while related species may mature at a small size, provide extended care, and be semelparous (Strathmann and Strathmann 1982).

recent models of parental care in nesting species (Gardner and Smiseth 2011), and reproductive spacing in non-parental (Ronce and Promislow 2010) and parental (Kindsvater et al. 2010) organisms. These insights, along with a decrease in adult mortality for nesting species that can promote a longer reproductive lifespan (Young 1990; Stearns 1992) provide an evolutionary pathway around the semelparity barrier for many subsocial invertebrates, and in a few groups, provided a first step to eusociality.

Methods

Standard phylogenetic contrasts to test the Semelparity Hypothesis are problematic for several reasons including a lack of a sufficiently detailed phylogeny for invertebrates, and, more importantly, a lack of data on the parental and parity state for most species. There is not even qualitative agreement on the parity state of most asocial insects. Price et al. (2011) considers "why insects are so often semelp-arous", while Fritz et al. (1982) and Tallamy and Schaefer (1997) feel that most species are iteroparous. Here, well-studied representative species are examined to assess: (1) whether iteroparity is common among care-giving species, contrary to the Semelparity Hypothesis; and (2) whether the type of care provided (nesting vs. open habitat care-givers) is associated with the parity state. A broad comparative test was employed using only cases for which there were data for both type of parental care and parity state. Costa's (2006) provides information from most insect families that exhibit a well-studied case of maternal care, as well as higher taxon treatments for other invertebrates. Using subheadings in Costa's work (usually at the family level), the single species (N = 65) in each section discussed in the most detail (assessed by the number of lines of text) that exhibited maternal care was chosen and categorized by parental care type and parity state. The use of one representative species per group reduced taxon bias. Because theoretical (Ranta et al. 2002) and empirical (Grosberg 1988; Meunier et al. 2012) work suggest that parity state can be labile within species, this analysis should include a large number of phylogenetically independent comparisons. Species were categorized as nesters, open habitat care-givers or carriers of young. Species in which the mother uses a nest, burrow, gall or silk structure were classified as a 'nester' regardless of whether it may follow young outside the nest or carry young. Species that cared for eggs or offspring exclusively outside such shelters were classified as 'open' care-givers whether or not they carry young. Ovoviviparous and viviparous species in which the mother carry hatched young were classified as a nester or open care-giver, if appropriate, and as 'carrier', if not (i.e., the mother does not use a nest and offspring are

not cared for more than 24 h once detached from the mother). There were few cases (N = 4) of exclusive carriers, so the results are included only in the overall totals. To obtain information on parity state, Costa (2006) was used as the primary reference. Where the state could not be determined from Costa, the literature was searched and investigators were queried.

Potential Biases

What are the potential biases in the analysis? (1) Reliance on Costa (2006) is not likely to favor an iteroparity-parental care outcome. Costa refers to Tallamy and Brown's (1999) Semelparity Hypothesis favorably ("I believe their hypothesis is largely borne out" p. 26). (2) The use of the best-studied examples is another potential source of bias. Because well-studied cases may be more likely to have extended or complex parental care (a reason for investigation), initially the bias would seem to favor the Semelparity Hypothesis because of the high level of investment in the brood (a secondary rationale in Tallamy and Brown's argument). (3) A third source of bias is the exclusion of eusocial insects in the Hymenoptera and Isoptera (not included in Costa (2006)), species that are typically iteroparous. (4) A fourth source of bias is that Costa (2006) only gives brief coverage to insects that retain young inside the body without providing additional care. For example, of the seven families of ectoparasites of vertebrates that are viviparous or pupiparous mentioned in Tallamy and Wood (1986), all are likely iteroparous (Arixeniidae and Hemimeridae [Dermaptera], Polyctenidae [Heteroptera], Hippoboscidae, Streblidae, Nycteribiidae and Glossinidae [Diptera]). (5) A final source of bias is the criteria for determining semelparity versus iteroparity. Species may be iteroparous if they produce non-overlapping broods (serial nesting if a nest is involved), or if oviposition continues while the mother continues to care for older offspring (within-nest iteroparity when a nest is involved). For within-nest iteroparity, a species was categorized as iteroparous if oviposition is spread out over greater than a 10-day period. While this duration is arbitrary, there was only a single species where it came into play. The open habitat *Atopozelus pallens* produces a series of egg masses estimated at 1.9 day intervals. It was classified as iteroparous, a classification supported by Tallamy et al. (2004). For serial nesters, different criteria were employed. Southwood (1977) suggested that reproduction in the laboratory is informative of parity in the field. Tallamy and Brown (1999) cautioned against the use of this criterion and labeled a species as effectively semelp-arous if it is unlikely to produce a second clutch in the field even if they produce two broods in the laboratory (contrary to Cole (1954)). It is agreed that a species such as the crab

spider *Lysiteles coronatus* (Futami and Akimoto 2005) should be considered semelparous because typically a second clutch is produced only if the first brood is interrupted before the young reach independence (e.g., by experimental removal). However, species that rear two separate broods to independence in the laboratory were classified as iteroparous. For example, Tallamy and Brown classify burying beetles as effectively semelparous because of the rarity of the resource necessary for reproduction (small carrion). While some smaller females may never breed in some years, larger females typically breed more than once, and most females may breed more than once in years with a high resource to female ratio. Most females can breed 3–5 times in the laboratory or protected in the field, and reproductive output does not decline until at least the third attempt (Scott and Traniello 1990; Cotter et al. 2010). As reasoned by Southwood (1977), this likely reflects selection to maintain the capacity for significant iteroparity to take advantage of favorable breeding conditions.

Statistical Analysis

To examine differences in iteroparity between nesting and open habitat species, *P* values (two-tailed) were calculated using Fisher's Exact Probability tests for 2 × 2 contingency tables (SAS 2007). To increase robustness, the analysis was done in four ways. The best described species was included for: (1) each subheading in Costa (2006); (2) each subheading for insects; (3) each subheading, excluding cases where the parity state was likely but not confirmed; and (4) each subheading at the family level or higher. In the latter analysis, the best-described species across the entire family was used as the representative data point.

Results

Of the 65 representative species exhibiting maternal care from Costa (2006) adequate information to classify parity state was found for 57. These are listed in Table 1 with their parity state and type of care (Nesting, Open Habitat, Carrier of Young). Of these 57 species, the majority (N = 44, 77.2 %) are likely or confirmed iteroparous. 53 of the 57 representative species were classified as either Nesting (including the use of galls, burrows and galleries) or Open care-givers. Nesters were more likely iteroparous than Open care-givers (87.9 vs. 55.0 % when using all section headings, Table 2). This difference was significant whether using all section headings, all family-level or higher headings (85.7 vs. 50 %), all insect headings excluding other arthropods (88.5 vs. 55.5 %), or all

headings excluding species for which the parity state was likely but not confirmed (86.7 vs. 56.3 %; all *P* < 0.05, Table 2).

Discussion

Iteroparity was found to be the predominant condition among studied invertebrates with parental care, especially for nesting species. The Semelparity Hypothesis (that parental care would be associated with semelparity among insects) was not supported in the broad sense. The narrow sense of the hypothesis (that among closely related populations or species those with greater parental investment would be associated with a decreased probability of future reproduction) was not tested; there currently is no theoretical reason to question it. Even though parental care on its own can cause semelparity, the opposite pattern becomes apparent in many groups on a broader phylogenetic scale (see Nagano and Suzuki (2008) for a narrow comparison of this transition showing a positive association of care and iteroparity). The transition from asocial to subsocial behavior may lead to other non-intuitive reversals of K-selected life history variables. For example, higher levels of parental investment decrease longevity in experimental manipulations (Gilg and Kruse 2003; Creighton et al. 2009), while a broader phylogenetic analysis of insects revealed a positive correlation between parental care and longevity (Carey 2001). Such reversals of life history correlations may be a frequent outcome of transitions between levels of social organization (Bourke 2011). Life history formulations associating parental care with iteroparity appear to apply to nesting terrestrial invertebrates. Because there is inadequate information on the parity state of asocial insects, it is not clear whether nesting behavior favors iteroparity to emerge from semelparity de novo or that it favors iteroparity to re-emerge after passing through a tendency toward semelparity.

This study also suggests that life history evolution operates differently in nesting species that provision offspring than in open-habitat subsocial species that guard or facilitate self-feeding by offspring (see Gilbert and Manica (2010) for differences between provisioners and guarders related to body size and fecundity). Since parental investment reduces future reproductive potential (Trivers 1972), the presumed association of parental care and semelparity was thought to be a weak link in models of the subsocial route to eusociality. The present study suggests that the rarity of subsocial groups that evolved eusociality is not due to the preponderance of semelparity (Alexander et al. 1991), but is likely due to other factors such as the stringent ecological conditions that favor offspring becoming non-reproductives (West et al. 2002; Wilson 2008).

Table 1 The parity state (I = iteroparity, S = semelparity) for invertebrates exhibiting extended parental care

Heading or subheading	Taxon	S/I	Type of care	Allocare by offspring	References
Dermaptera					
Labiduridae	*Labidura riparia*	I	N (Ser)		Vancassel (1984)
Forficulidae	*Forficula auricularia*	I	N (Ser)		Lamb (1976)
Anisolabididae	*Euborellia annulipes*	I	N (Ser)		Rankin et al. (1996)
Spongiphoridae	*Labia minor*	I	N (Ser)		Mourier (1986)
Orthoptera					
Gryllidae	*Anurogryllus muticus*	S	N (–)		West and Alexander (1963)
Embiidina					
Oligotomidae	*Oligotoma* spp	I[a]	N(W)	Expand gallery?	Ananthasubramanian (1956)
Embiidae	*Embia ramburi*	I	N(W)	Expand gallery?	Ledoux (1958)
Clothodidae	*Antipaluria urichi*	S	N (–)		Edgerly (1997, pers. comm.)
Mantodea					
Tarachodidae	*Tarachodes maurus*	I	O		Ene (1964)
Blattodea					
Blaberidae—Panesthiinae	*Panesthia cribrata*	I	N (Ser)		Rugg and Rose (1990)
Blaberidae—Geoscapheinae	*Macropanesthia rhinoceros*	I	N (Ser)		Rugg and Rose (1991)
Blaberidae—Blaberinae	*Byrsotria fumigata*	I	O		Barth and Bell (1970)
Blaberidae—Epilamprinae	*Thorax porcellana*	I	C		Bhoopathy (1998)
Blaberidae—Diplopterinae	*Diploptera punctata*	I	C		Stay and Tobe (1977)
Blaberidae—Oxyhaloinae	*Nauphoeta cinerea*	I	C		Barrett et al. (2008)
Blaberidae—Perisphaerinae	*Perisphaerus* spp	I[a]	C		Roth (1981)
Cryptocercidae	*Cryptocercus punctulatus*	S	N (–)		Nalepa (1984)
Psocoptera					
Peripsocidae	*Peripsocus nitens*	I	O		New (1985)
Archipsocidae	*Archipsocus* spp.	I	N(W)	Construct and repair web	Mockford (1957)
Zoraptera					
Zorotypidae	*Zorotypus* spp.	I	N (Ser)		Choe (1997)
Hemiptera					
Pemphigidae	*Smynthurodes betae*	I	N(W)	Defense	Inbar (1998, pers. comm.)
Membracidae—Hoplophorionini	*Umbonia crassicornis*	S	O		Wood (1976)
Membracidae—Aconophorini	*Guayaquila compressa*	S[a]	O		Wood (1978)
Membracidae—Membracini	*Erechtia sallaei*	I[a]	O		Lin (2006)
Membracidae—Polyglyptini	*Publilia reticulata*	I	O		Bristow (1983)
Acanthosomatidae	*Elasmucha grisea*	S	O		Mappes et al. (1995)
Pentatomidae	*Antiteuchus tripterus*	I	O		Eberhard (1975)
Cydnidae	*Sehirus cinctus*	I	N (Ser)		Kight (pers. comm.)
Reduviidae	*Atopozelus pallens*	I[a]	O		Tallamy et al. (2004)
Tingidae	*Gargaphia solani*	I	O		Tallamy and Horton (1990)
Thysanoptera					
Phlaeothripidae—Idolothripinae	*Elaphrothrips tuberculatus*	I	O		Crespi (1989)
Phlaeothripidae—Phlaeothripinae	*Oncothrips* spp.	I	N(W)	Defense	Crespi (1992)
Coleoptera					
Scarabaeidae	*Canthon cyanellus*	I	N (Ser)		Halffter and Edmonds (1982)
Passalidae	*Odontotaenius disjunctus*	I	N(W)	Facilitate digest., assist pupation	Schuster and Schuster (1997)
Staphylinidae—Aleocharinae	*Eumicrota socia*	I[a]	N (Ser)		Ashe 1986
Staphylinidae—Oxytelinae	*Bledius spectabilis*	I	N (Ser)		Wyatt and Foster (1989a, b)

Table 1 continued

Heading or subheading	Taxon	S/I	Type of care	Allocare by offspring	References
Silphidae	*Nicrophorus defodiens*	I	N (Ser)		Cotter et al. ([2010])
Curculionidae—Scolytinae	*Ips pini*	I	N (Ser)		Reid and Roitberg ([1994])
Curculionidae—Platypodinae	*Austroplatypus incompertus*	I	N(W)	Hygiene, expand gallery	Kent and Simpson ([1992])
Curculionidae—Cryptorhynchinae	*Tentegia ingrata*	I	N (Ser)		Wassell ([1966])
Chrysomelidae—Chrysomelinae	*Gonioctena* spp.	S	O		Kudô et al. ([1995])
Chrysomelidae—Cassidinae	*Acromis sparsa*	I	O		Windsor and Choe ([1994])
Silvanidae	*Coccidotrophus socialis*	I	N(W)	Maintain domicile	Wheeler ([1921])
Tenebrionidae	*Parastizopus armaticeps*	I	N(W)	Facilitate feeding	Rasa ([1998])
Lepidoptera					
Nymphalidae	*Hypolimnas anomala*	S	O		Schreiner and Nafus ([1991])
Hymenoptera					
Pamphilidae	*Cephalcia isshikii*	S	O		Kudô et al. ([1992])
Tenthredinidae	*Nematus tiliae*	S	O		Kudô et al. ([1998])
Argidae	*Dielocerus diasi*	S[a]	O		Dias ([1976])
Non-insects					
Araneae	*Anelosimus studiosus*	I	N(W)	Prey capture, web building	Jones and Parker ([2002])
Amblypygi	*Phrynus* spp.	I	O		Rayor and Taylor ([2006])
Opiliones	*Goniosoma* spp.	S	O		Machado and Oliviera ([1998])
Pseudoscorpionida	*Paratemnoides nidificator*	I	N (Ser)		Tizo-Pedroso and Del-Claro ([2005])
Scorpionida	*Heterometrus fulvipes*	I	N(W)	Prey capture, excavate tunnel	Shivashankar ([1994])
Acari	*Stigmaeopsis longus*	I	N(W)	Defense, construct domicile	Mori and Saito ([2004])
Chilopoda—Geophilomorpha	*Dicellophilus carniolensis*	I[a]	N (Ser)		Bonato and Minelli ([2002])
Isopoda	*Hemilepistus reaumuri*	S	N (–)		Linsenmair ([1987])
Decapoda	*Metopaulias depressus*	I	N(W)	None known	Diesel ([1989])

For iteroparous nesters, within-nest (W) and serial nesting (Ser) iteroparity are indicated. Parity state and notes on allocare for within-nest iteroparous species from Costa ([2006]) and indicated references

N nesting, *O* care-giving in open without nesting, *C* carrier of offspring without a nest and without subsequent care when offspring detached

[a] The trait (semelparity vs. iteroparity) is based on indirect evidence, or direct evidence from a congener with a similar level of care. No adequate information was available for *Gryllotalpa* [=*Neocurtilla*] *hexadactyla*, *Anisembia texana*, *Physomerus grossipes*, *Phloe* spp., *Pygoplatus* spp., *Pselaphacus* spp., *Cladomacra* spp., and *Dicrocheles phalanodectes*

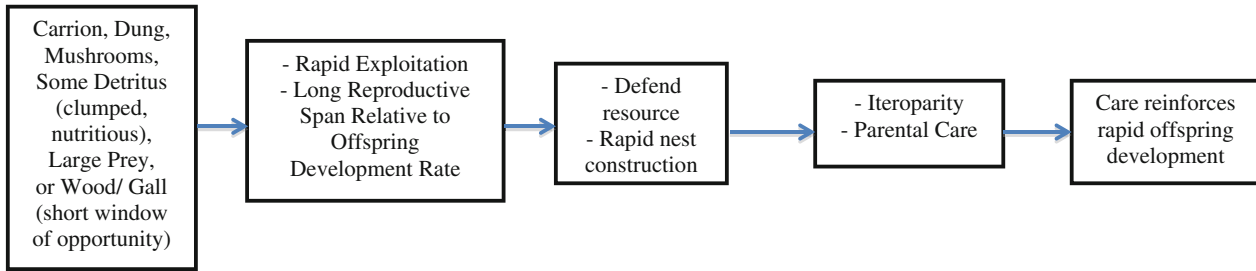**Table 2** Relationship between parity state and nesting versus open habitat care-giving for species from Table [1]

	All subheadings		Insect-only subheadings		All subheadings excluding 'likely' data		Subheadings at family level or above	
	Nest	Open	Nest	Open	Nest	Open	Nest	Open
Iteroparous	29	11	23	10	26	9	24	7
Semelparous	4	9	3	8	4	7	4	7
	$P = 0.01$		$P = 0.031$		$P = 0.032$		$P = 0.024$	

P values from fisher's exact test of 2×2 contingency tables

Why is iteroparity common among nesting invertebrates with parental care when withholding resources for the future is risky? There are three possible explanations for the iteroparity-parental care association: (1) iteroparity selects for care; (2) care selects for iteroparity; or (3) both

care and iteroparity are selected by the same set of life history/ecological variables. The first (1) possibility is the opposite of Tallamy and Brown's ([1999]) primary rationale (semelparity can lead to care) and seems unlikely because iteroparity, in itself, should not allow more resources to be

(a) – Serial nesting

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┌──────────────┐   ┌──────────────┐   ┌──────────────┐   ┌──────────────┐   ┌──────────────┐
│ Carrion, Dung,│   │- Rapid       │   │- Defend      │   │- Iteroparity │   │Care reinforces│
│ Mushrooms,   │   │ Exploitation │   │ resource     │   │- Parental Care│  │rapid offspring│
│ Some Detritus│ → │- Long Reprod.│ → │- Rapid nest  │ → │              │ → │development    │
│ (clumped,    │   │ Span Relative│   │ construction │   │              │   │              │
│ nutritious), │   │ to Offspring │   └──────────────┘   └──────────────┘   └──────────────┘
│ Large Prey,  │   │ Development  │
│ or Wood/Gall │   │ Rate         │
│ (short window│   └──────────────┘
│ of opportun.)│
└──────────────┘
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(b) – Within-nest iteroparity or nesting with semelparity
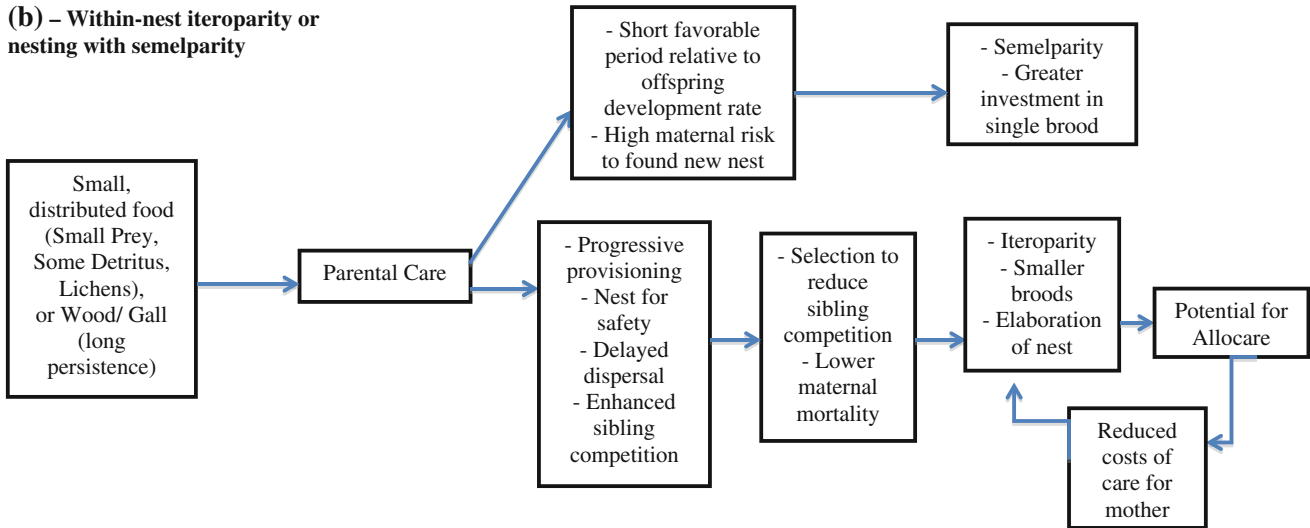
Fig. 1 Correlation of iteroparity and parental care in nesting species: **a** Mutual factors (resource type and selection for rapid exploitation) favor both serial broods and care (serial nesting): **b** Parental care as an indirect cause of within-nest iteroparity by selecting for increased reproductive spread to reduce sibling competition, and by selecting for delayed dispersal of offspring

devoted to the current brood. The second (2) is the opposite of the secondary rationale of Tallamy and Brown (care reduces the potential for future reproduction). Despite the negative effect of care on future reproduction, there may be indirect paths from care to iteroparity that can explain within-nest iteroparity. For serial nesters and species that carry offspring, it is hypothesized that common factors (3) caused both serial broods (iteroparity) and care. These possibilities are outlined in Fig. 1.

Within-Nest Iteroparity

For within-nest iteroparity, recent models by Gardner and Smiseth (2011), Ronce and Promislow (2010), and Kinds-vater et al. (2010) suggest how care could select for iteroparity. A nesting female can choose a nest site based on safety or proximity of food. Gardner and Smiseth (2011) have modeled the transition from guarding self-feeding young to provisioning food for young. After the evolution of food provisioning, mothers are less constrained in the selection of a nest site and can select primarily on safety.

During this transition, parental care effectiveness becomes more dependent on the density of young, thereby increasing competition among siblings. This altered social environment acts to selectively reinforce parental provisioning behavior (see also Van Dyken and Wade 2012a) and attendance to offspring (Gardner and Smiseth 2011). Feeding within a safe nest can also select for delayed dispersal of offspring (Wyatt and Foster 1989a; Alexander et al. 1991), a common mechanism for social evolution, also present in vertebrates (Davis et al. 2011; Cant 2012). Lower juvenile mortality further increases conflict for food and space. Alexander (1974) suggested that parental manipulation to induce allocare might reduce deleterious sibling competition when offspring remain in the nest for a longer period (also see Crespi and Ragsdale 2000). These explanations, however, presuppose both iteroparity and incipient allocare.

How does enhanced sibling competition lead to iteroparity? In a model for species without parental care, Ronce and Promislow (2010) demonstrated that where siblings compete with each other or with their parent (limited

dispersal of offspring), selection will act to spread out reproduction over the parent's lifetime, reducing sibling conflict and slowing maternal reproductive senescence. Kindsvater et al.'s (2010) state-dependent model that is general for parental and nonparental species likewise predicts that sibling competition will select for fewer offspring at one time, spreading out offspring over the reproductive lifespan of the mother.

When offspring are highly dependent on their mother's survival, however, there is a risk that she dies before offspring reach independence (Field and Brace 2004). Modeling human reproduction, Pavard et al. (2007) found that offspring dependence on a sole care-giver can decrease early and late fertility, increasing late survival and narrowing the period of peak fertility. A female thus increases the probability that she will survive her offspring's long dependent period by decreasing inter-birth intervals (the model neglects sibling competition). In species with extended parental care then, there appears to be a tension between reducing family conflict by spreading out reproduction, and increasing the probability of maternal presence throughout the juvenile dependent period by shortening the reproductive span.

Among species with less sibling competition, as in a non-nesting parent that guards offspring in the open, effectiveness of care is less density dependent and care is more efficient when young hatch synchronously. The tension is less and semelparity is more likely. An invertebrate mother guarding different-aged cohorts of post-hatching offspring in the open is quite rare. Most iteroparous species that care in the open guard eggs (either non-overlapping or overlapping clutches) or carry eggs prior to guarding (serial clutches). Because a high percentage of asocial folivores may be iteroparous (Tallamy and Schaefer 1997), open habitat subsocial insects appear to be a good fit for Tallamy and Brown's (1999) conception of care and semelparity.

In nesting species, however, sibling competition can have important effects, especially when there is food provisioning (Gardner and Smiseth 2011). Selection to reduce clutch size and extend the period of brood production (Kindsvater et al. 2011), can increase offspring access to food and space, promoting delayed dispersal. Just as the physical spacing of offspring can evolve so that family structure reduces conflict (Royle et al. 2012), so may it be with temporal spacing of offspring. The mother herself may feed within the safety of the nest, decreasing maternal mortality and further extending the reproductive span (Stearns 1992). The dynamics often favor iteroparity with different-aged offspring within the nest. This may account, in part, for the slower rate of reproduction and longer adult life in nesting species with provisioning, trends previously ascribed to population, not family, competition (Nevo 1979; Hansell 1996). Models that incorporate both kin

competition and parental assistance to young are likely to provide additional insight on the importance of nesting for the evolution of iteroparity and eusociality (Ronce and Promislow 2010).

Where nests are elaborately constructed, production of an initial small brood by an iteroparous nester before a nest has reached its final size can also allow a female to obtain a partial reproductive benefit. A semelparous nester that delays brood production until a nest is complete risks losing the sunk costs of nesting effort to nest failure before any fitness gains are realized. Field and Brace (2004) similarly consider the ability of iteroparous progressive provisioners to terminate a bad investment with less cost than mass provisioners. In some groups, the problem of surviving the dependent period of offspring could be lessened by joint nesting of co-foundresses, one of which is likely to survive the requisite period, reducing selection to minimize the spread in reproduction. This scenario, however, also assumes allocare by co-foundresses at the outset (Queller 1996).

Allocare

The resolution of social conflict may permit the subsequent evolution of new social traits (Bourke 2011). Modelers have recognized the importance of nesting and subsocial behavior as preconditions for the evolution of eusociality (Hansell 1987; Nowak et al. 2010). Some have also stressed allocare by older siblings for younger siblings (Alexander 1974; Linksvayer and Wade 2005) but how or why subsocial nesters should produce offspring of different ages before allocare first evolved is rarely considered. The production of smaller, multiple cohorts of young can reduce conflicts of interest among siblings without coercion or manipulation. Smaller broods are also characteristic of cooperatively breeding birds with delayed dispersal of older offspring (Arnold and Owens 1998). A smaller brood size can also lessen peak demand on the mother, reducing maternal mortality and prolonging the duration of the reproductive span. Such iteroparity within the nest is a precondition for age-based allocare by siblings. The potential for allocare, however, is not the driving force for iteroparity. After iteroparity evolves, older offspring that delay dispersal can benefit younger siblings without extensive behavioral innovation, being as simple as expanding the nest, occupying a gall entrance or passive transfer of digestive symbionts (Mockford 1957; Kent and Simpson 1992; Nalepa 1994; Avilés 1997; Saito 1997; Tizo-Pedroso and Del-Claro 2005; Bierdemann and Taborsky 2011). Initially, there may be no cost for such byproduct benefits. Examples of more costly allocare for species with within-nest iteroparity are given in Table 1. At its inception, true allocare may be built upon

phenotypically plastic responses of young (Hunt 2012) to variable social environments imposed by differences in nutrition, brood size and age of offspring. Selection might then operate to redirect care toward younger sibs rather than to offspring (Hunt and Amdam 2005), or to protect the common nest. Such indirect reproductive gains can be obtained more quickly than the direct benefits of establishing a new nest as a solitary breeder (Nonacs 1991; Queller 1996). Once offspring evolve to assume some costs of parenting, the increase in maternal survival rate and the care-giving insurance provided by allocare (Gadagkar 1990; Bull and Schwarz 2012) may further reduce selection on the mother to minimize the spread in reproduction. The production of multiple broods can then be timed to better maximize benefits from allocare; in more complex cooperative societies, the trend toward smaller families is likely to reverse (Bourke 2011). Eusocial insects exhibiting within-nest iteroparity are the ecologically dominant animals in most ecosystems (Wilson 2008).

Serial Nesting

Selection for reduction of sibling competition and delayed dispersal of offspring may account for the preponderance of iteroparity among species that construct a single nest, but not for the dung roller, *K. nigroaeneus*, nor for other serial nesters that produce a single brood per nest. In many species that exploit high-quality food, both care and iteroparity may have been selected in response to other common factors, particularly rapid juvenile development (Klug and Bonsall 2009). In dung beetles, burying beetles, and mushroom nesters, a female or male–female pair constructs a burrow or nest that not only protects offspring, but also secures access to a valuable and ephemeral resource. The high frequency of biparental care in these groups is likely a response to better pre-empt and defend the resource against competitors (Wilson 1971; Trumbo 2006). Among serial nesters utilizing a valuable resource, brood size may be less constrained by nutritional resources that can be devoted to fecundity and more by ecology (the size of the resource that can be located and manipulated, the number of offspring that can be cared for, and selection for large-bodied competitive offspring). Costs of maternal care are often reduced in these species by rapid development of young, necessitated by the threat of predators and competitors and facilitated by highly nutritious food (Ashe 1986; Trumbo 2012). Costs to the mother can be further reduced by the ability to feed herself without leaving the nest, and sometimes by the help of a male (Jenkins et al. 2000). In some species, rapid development is also facilitated by regurgitation to young (Edwards and Aschenborn 1989; Smiseth and Moore 2007; Staerkle and Kölliker 2008). A rapid parental cycle and reduced maternal costs

increase the probability that selection favors females that can take advantage of a renewing crop of resources.

Subsocial insects that utilize less protein-rich resources such as detritus and wood do not fit into a single parity state. Detritivores may be semelparous (*Anurogryllus*, Gryllidae), serial nesters that construct a new nest for each brood (Dermaptera), serial nesters that re-use a nest (*Bledius* spp., Staphylinidae), iteroparous species that carry young (some cockroaches) and within-nest iteroparous species (*Parastizopus armaticeps*, Tenebrionidae) (Table 1). Some behavioral variation may be explained by variation in clumping, portability and nutritional value of the detritus. Behavioral variation among wood feeders can often be related to the duration of the window of opportunity for optimal resource exploitation, and the subsequent persistence of the resource. This period is quite brief for the serial nesting *Ips* spp. while the eusocial *Austroplatypus incompertus* (Curculionidae) exploits live trees that can sustain generations of offspring (Table 1).

Semelparity Among Nesters

The opportunity cost of semelparity is that a female that could achieve a positive energy balance over a predictable future foregoes the possibility of turning pulses of resources into a series of broods. We would expect semelparity among nesting species then, only when resources are available for a short period of time, separated by a lengthy, unfavorable period with a high probability of extrinsic mortality. For example, among the Cydnidae, *Parastrachia japonensis* provisions its nest with fruits that are produced 'erratically and asynchronously' (Costa 2006). In typical semelparous fashion, the female dies soon after offspring independence (Filippi et al. 2001). In *Sehirus cinctus* (Sites and McPherson 1982) and *Adomerus rotundus* (Mukai et al. 2010), however, resources are more predictable during the breeding season and females can produce more than one brood. Similarly, for most iteroparous dung, carrion and mushroom feeders, although the exact time and location of an available resource is unknown, there is a renewing supply of resources for which to compete during a lengthy period (relative to the nesting cycle) of favorable environmental conditions.

In Table 1, two of the exceptions to the nesting-iteroparity association (*Antipaluria urichi* [Clothodidae] and *Cryptocercus punctulatus* [Cryptocercidae]) are found in taxonomic groups with a mixture of iteroparous and semelparous species. The embiids construct silken galleries over lichen patches that serve as food for their young. Semelparity in *A. urichi* may occur because the female does not provision lichen for young and offspring do not expand the nest. The mother feeds little as the gallery system is completed, sacrificing her nutritional needs for

her young. The high risk of starting a new gallery system may also be too high to favor serial nesting (Edgerly, pers. comm.). In other embiids in which food is gathered and the parent and/or young expand the gallery system, there are often cohorts of different-aged offspring found within the same nest (Edgerly 1997, Edgerly, pers. comm.). The temperate zone semelparous wood roach *C. punctulatus*, regarded as a model for the evolution of early termites (Nalepa 1994), has a low efficiency of energy extraction from wood and a limited growing season. The long juvenile developmental period might make iteroparity difficult. The iteroparous tropical wood cockroaches *Panesthia* spp. have an even longer juvenile period but this is matched by an extraordinary 4–5 year adult reproductive period in which a new brood is typically produced each year (Rugg and Rose 1990). Among temperate zone wood-feeding passalid (Passalidae) and ambrosia beetles (Curculionidae), iteroparity occurs along with considerably faster juvenile development (Kirkendall et al. 1997; Schuster and Schuster 1997). The use of wood has led to iteroparity and social behavior beyond simple parental care in several lineages. Contributing factors are likely the low extrinsic mortality rates in a long-lasting shelter where outside foraging is not necessary, delayed dispersal of offspring, selection to reduce sibling competition, and the ability of older siblings to benefit younger siblings at little cost. Colder and drier environments both shorten the favorable season for breeding and lengthen the unfavorable season for most invertebrates. Most earwigs (Dermaptera) are apparently iteroparous. The montane *Aneuchuria harmandi* (Kohno 1997) and high elevation populations of the typically iteroparous *Forficula auricularia* (Wirth et al. 1998), however, are semelparous.

Other Paths to Iteroparity: Iteroparity Among Non-nesters

An alternative pathway to iteroparity can evolve in species where the cost of maternal care can be reduced by off-loading care to other individuals. In the present analysis, species with exclusive paternal care and those in which ant attendance is obligatory for the survival of young were excluded. The analysis, however, did include three open-guarding iteroparous species that facultatively offload care to a conspecific (*Gargaphia solani* (Tingidae), Tallamy and Horton 1990) or to ants (*Publilia reticulata*, Bristow 1983; *Erechtia sallaei* (Membracidae), Lin 2006). This is consistent with Tallamy and Brown's (1999) Semelparity Hypothesis where the reduced costs of reproduction favor iteroparity. If these species were to be excluded from the analysis, the statistical contrast between nesting and open care-givers would be more pronounced.

Iteroparity was found in the four species in Table 1 that carry their young, and is also apparently common in the viviparous and pupiparous ectoparasites listed in Tallamy and Wood (1986), and in crustaceans that carry their young for an extended period (Thiel 2000). In these cases the body size of the mother may limit the number of young that can be cared for, diminishing the fecundity advantage of semelparity. Tallamy et al. (2004) also suggest that where mothers have the opportunity to feed during care-giving, such as in the open habitat guarders *A. pallens* (Reduviidae), *Elaphrothrips tuberculatus* (Phlaeothripidae) and *Peripsocus nitens* (Peripsocidae) (Table 1), iteroparity may be more common. The direction of causation for an iteroparity-maternal feeding association could go in either direction, or be mutually reinforcing.

Future Directions

A comprehensive understanding of parental care in insects will need to address why extended parental care is so rare in this group. Tallamy and Brown (1999) have reasoned that this is partly due to the modest benefits of care in many small organisms, in particular the lack of ability to defend resources or construct nests. The effective stings, venoms and poisons common among non-insect invertebrates (and in Hymenoptera) have provided more opportunity for effective care-giving. Among insects, an effective ovipositor and remarkable egg adaptations have minimized the added value of extended care (Zeh et al. 1989). While rare, the particular combinations of resources, environments and preadaptations that do favor parental care, either also favor iteroparity (serial nesters and carriers of young), or led to a favorable family environment for iteroparity (within-nest) to evolve or re-evolve.

Phylogenetic contrasts are needed to test the hypotheses presented here: (1) that iteroparity is the predominant pattern among parental insects; (2) that iteroparity is more common among nesting subsocial invertebrates than species that guard young (especially mobile young) in the open; and (3) that carrying young internally or externally is associated with iteroparity. Contrasts can also test hypotheses from Tallamy and Brown (1999) and Tallamy (2005) that (1) maternal feeding during care and (2) the ability to transfer the costs of care to others, promote iteroparity. Information is needed on parity state for both asocial and subsocial species, over which there is much disagreement (Fritz et al. 1982; Costa 2006; Price et al. 2011). Comparisons should not be restricted to experimental manipulations and narrow phylogenetic contrasts that typically show a greater tendency toward semelparity with greater parental investment. The present study demonstrates that a transition between levels of social organization can alter expected life history correlations. In

particular, the evolutionary transition from an asocial to a subsocial state has created selection pathways around the semelparity barrier for many insects that led to iteroparity within the nest, some of which gave rise to the most ecologically dominant animals. The present study also shows that protection of valuable resources that nutritionally support rapid larval development has led to both parental protection and serial nesting. These associations are predicted to be evident in future broad-scale phylogenetic comparisons.

Conflict of interest The author declares no conflict of interest.

Ethical Statement This work complies with the laws of the state of Connecticut and the United States of America.

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