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COMMUNAL EGG-LAYING IN REPTILES AND AMPHIBIANS: EVOLUTIONARY PATTERNS AND HYPOTHESES

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KEYWORDS

conspecific cueing, oviposition site choice, game theory, evolutionary stable strategy, egg aggregations

*Many reptiles lay their eggs together in the most suitable sites, but it is difficult to account for the colonial nesting habit . . . without assuming that the gravid females are in some way attracted by the eggs of their own species.
(Noble and Mason 1933:13)*

ABSTRACT

Communal egg-laying is widespread among animals, occurring in insects, mollusks, fish, amphibians, reptiles, and birds, just to name a few. While some benefits of communal egg-laying may be pervasive (e.g., it saves time and energy and may ensure the survival of mothers and their offspring), the remarkable diversity in the life histories of the animals that exhibit this behavior presents a great challenge to discovering any general explanation. Reptiles and amphibians offer ideal systems for

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investigating communal egg-laying because they generally lack parental care—a simplification that brings nest site choice behavior into sharp focus. We exhaustively reviewed the published literature for data on communal egg-laying in reptiles and amphibians. Our analysis demonstrates that the behavior is much more common than previously recognized (occurring in 481 spp.), especially among lizards ($N = 255$ spp.), where the behavior has evolved multiple times. Our conceptual review strongly suggests that different forces may be driving the evolution and maintenance of communal egg-laying in different taxa. Using a game theory approach, we demonstrate how a stable equilibrium may occur between solitary and communal layers, thus allowing both strategies to co-exist in some populations, and we discuss factors that may influence these proportions. We conclude by outlining future research directions for determining the proximate and ultimate causes of communal egg-laying.

ANIMAL AGGREGATIONS have been the focus of a large body of scientific literature since Allee's (1927) early seminal review, and considerable attention has been focused on examining their adaptive value (Hamilton 1971; Treisman 1975; Turner and Pitcher 1986; Inman and Krebs 1987). It is generally assumed that whether an organism aggregates or not is dependent upon associated fitness costs and benefits as determined by natural selection, although passive processes, such as a shortage of environmental conditions, may result in inadvertent aggregations as well (Wrona and Dixon 1991).

Animal egg aggregations have received less attention and have generally been a poorly understood form of social reproduction in vertebrates (Danchin and Wagner 1997). The choice of egg-laying site can be an important component of fitness, especially in animals without parental care (Howard 1978; Resetarits and Wilbur 1989; Resetarits 1996). For example, oviposition site choice can have a profound influence on environmental conditions critical to developing embryos and offspring phenotypes (Deeming and Ferguson 1991; Resetarits 1996; Birchard 2004), and can also influence the probability that eggs may fall victim to predation (Howard 1978; Petranka and Fakhoury 1991). According to Resitarits (1996), what has been largely missing from current life history theory is the consideration of female oviposition site choice in the evolution of life histories.

Communal egg-laying (also referred to as communal nesting, joint nesting, colonial nesting, communal oviposition, or egg dumping), whereby animals deposit their eggs or young with those of conspecifics, is

taxonomically widespread among animals (mammals: Hayes 2000; birds: Emlen 1982; reptiles: Graves and Duvall 1995; frogs: Howard 1980; salamanders: Harris and Gill 1980; fish: Huggins and Thompson 1970; gastropods: Ilano et al. 2004; dragonflies: Martens and Rehfeldt 1989; mayflies: Peckarsky et al. 2000; beetles: Damman and Cappucino 1991; caddisflies: Hoffman and Resh 2003; lacebugs: Loeb and Bell 2006; treehoppers: Zink 2005; flies: Zwick and Zwick 1990; bees: Myers and Loveless 1976; butterflies: Godfray et al. 1991). The antiquity and persistence of nesting aggregations is evident in their occurrence among some dinosaurs (Horner 1982; Carpenter et al. 1994; Carpenter 1999; Horner 2000).

Although hypotheses have been raised as to why communal egg-laying occurs in some groups (e.g., Ward and Kukuk 1998; Tallamy 2005), the adaptive value of this behavior in the vast majority of cases remains unclear (Danchin and Wagner 1997). The remarkable diversity in the life histories of these groups presents a great challenge to discovering any generality for communal egg-laying. For example, while communally nesting birds might be expected to benefit from assistance in provisioning offspring, this benefit would not apply to animals whose mothers generally abandon the nest shortly after oviposition. In a more complex example, in one communally egg-laying insect, mothers are faced with balancing trade-offs, such as leaving the nest to forage versus eating the egg of a conspecific and then replacing the eaten egg with one of their own (Ward and Kukuk 1998). The selective regimes associated with communal egg-laying are thus likely to differ among groups with diverse attributes, such as parental care (e.g., mammals, birds), brood parasitism (e.g., gastro-

ods, hemipterans, coleopterans, bees, fish, birds), communal spawning (e.g., fish), male interference (e.g., dragonflies), and host plant specificity (e.g., butterflies). Despite this, some benefits of communal egg-laying may be pervasive, such as a reduction in predation risk (Foster and Treherne 1981; Sweeney and Vannote 1982) or a savings in effort associated with egg-laying (Wiewandt 1982; Danforth 1991).

Reptiles and amphibians can serve as models for investigating the causes, costs, and benefits of communal egg-laying without the confounding factors associated with parental care. For example, parental care occurs in only 20% of salamanders, 6% of frogs, 3% of snakes, and 1% of lizards and turtles (Shine 1988; Iverson 1990; Crump 1995). Other potentially confounding factors, such as broadcast spawning, male interference, and host plant specificity, are also absent in reptiles and amphibians. This simplifies our ability to determine the advantages that communal egg-laying confers to mothers or offspring and also focuses our attention on oviposition site choice behavior. Although genetic variation in oviposition site choice behavior has not been demonstrated for reptiles and amphibians, there is evidence for its heritability in insects, including additive polygenic inheritance for communal laying in *Drosophila* (reviewed in Messina 1998). Reptiles offer a further advantage because mating and oviposition are temporally—and thus spatially—uncoupled, thereby eliminating the confounding factor of mate choice on oviposition site selection.

The prevalence of communal egg-laying in reptiles and amphibians has not been comprehensively reviewed. Graves and Duvall (1995), in an insightful review of aggregation behavior in squamate reptiles, found communal egg-laying in 60 lizard spp. and 20 snake spp., but these numbers comprised $\leq 1\%$ of all species in both groups. However, the eggs of these secretive animals are often unknown because they are difficult to find (Tinkle 1967; Juterbock 1986; Shine 1988; Perry and Dmi'el 1994; Andrade et al. 2006). This

almost certainly results in the underestimation of the incidence of communal egg-laying, and a more accurate analysis would determine the number of known communal layers as a proportion of the total for which the eggs or nests are known.

Why do some reptiles and amphibians lay communally? While some researchers have suggested that communal egg-laying may result from a shortage of nest sites (Vitt 1993; reviewed in Graves and Duvall 1995), a growing body of evidence indicates that communal egg-laying may serve some type of adaptive function, and this is based on two important observations: (1) communal clutches are frequently observed in areas with an apparent abundance of nest sites (Graves and Duvall 1995; Doody 2006), and (2) conspecific cueing has been demonstrated in the laboratory for nesting snakes and lizards (Plummer 1981; Brown and Shine 2005; Radder and Shine 2007) and in the field for ovipositing frogs (Howard 1980; but see Seale 1982). Thus, it is essential to consider adaptive explanations and to identify the benefits, costs, causes, and correlates of communal egg-laying. For instance, most species exhibiting communal egg-laying are also known to lay eggs in isolation, and this dichotomy often occurs within the same population (Vitt et al. 1997; Herreid and Kinney 1967). Do some individuals invariably lay communally while others always lay in isolation, or is communal egg-laying context-dependent? Under what context would these individuals lay communally? How might communal egg-laying persist in populations in which the chances of discovering the nest of a conspecific are limited?

In this review, we address these questions by reviewing communal egg-laying behavior in reptiles and amphibians and by evaluating the evidence for the hypotheses generated to explain its evolution. We give particular attention to lizards, where the behavior is most common. Using a game theory model, we demonstrate how both solitary and communal egg-layers can coexist in certain populations at any given time, and also how to predict the fre-

quency of communal layers within a population. Finally, using conceptual models, we suggest directions for future studies that would ultimately determine the significance of communal egg-laying in reptiles and amphibians, as well as in other animals lacking parental care.

SCOPE OF THE REVIEW: WHAT CONSTITUTES COMMUNAL EGG-LAYING IN REPTILES AND AMPHIBIANS?

“Communal nesting” is often used to describe different phenomena. In higher vertebrates, the term often refers to multiple individuals rearing young in a single nest (Manning et al. 1995; Hayes 2000). However, in mammals, the term often includes winter aggregations or “huddling groups” that apparently reflect behavioral thermoregulation (Layne and Raymond 1994). For reptiles and amphibians, we define this phenomenon as a clumped distribution of egg clutches at a scale visible to an observer, whereby it is highly likely that mothers would have detected the presence of conspecific eggs or conspecific mothers during oviposition site choice. We chose to use “communal egg-laying” rather than “communal nesting” because reptiles and amphibians often do not construct nests (Zug et al. 2001; Pough et al. 2004). We recognize a continuum of nesting effort, with species at one end expending considerable time and energy in the actual nest excavation (Burger and Zappalorti 1991; Mora 1989), while those at the other end simply add their eggs to existing eggs without any nest construction (Wells 1977; Roberts 1994). Also, our definition is not restricted to simultaneous laying by conspecific mothers, despite the terminology.

In reptiles, two basic types of communal egg-laying are often distinguished, based upon scale. Following the guidelines set forth by Espinoza and Lobo (1996), “communal nesting” refers to mothers laying their eggs with those of conspecifics under or within structures such as rocks, logs, bark, vegetation, or crevices, whereas “colonial nesting” involves mothers utilizing common nesting areas, but, in this case, the eggs are often buried and generally not

visible to conspecifics. It is sometimes important to distinguish between these two forms of communal egg-laying because colonial nesters often dig up the eggs of conspecifics (Wiewandt 1982; Rand and Dugan 1983; Mora 1989). We are careful to distinguish between the two forms in our review of the incidence of communal egg-laying because the latter can incur a unique cost associated with the destruction of previously laid eggs, but, in our conceptual review, we refer to both forms simply as “communal egg-laying” because similar processes likely unite them, and also because we do not deal directly with measuring the costs of communal egg-laying. In our discussion of amphibians, we use the terms communal oviposition, communal nesting, and joint nesting (e.g., Waldman 1982; Zina 2006; Harris 2008).

Some reptiles and amphibians are viviparous, and the causes, cues, and advantages associated with “communal gestation” in viviparous species could be similar to those associated with communal egg-laying in oviparous species. However, this behavior is apparently less common than communal nesting in oviparous species and may require synchronicity of mothers in one place, whereas communal egg-laying does not (Graves and Duvall 1995). We therefore restrict our review to oviparous species but acknowledge that similar processes may be at work in viviparous species. Finally, while parental care in reptiles and amphibians is rare, it nevertheless occurs among some species in each group (Reynolds et al. 2002), and such parental care is typically limited to egg attendance or egg guarding in these instances (Zug et al. 2001; Pough et al. 2004). Our review indicates that communal egg-laying may be seen in some species with attending mothers (Harris and Gill 1980; Cooper et al. 1983; Ovaska et al. 1998), thus indicating that the two are not always mutually exclusive. We have included those cases in our review, and we discuss how they might differ from the more typical communal egg-laying cases in species lacking parental care (see Harris 2008 for a comprehensive treat-

ment of the behavior in an attending salamander).

We conducted an extensive review of the relevant published literature, including primary journals and regional herpetological journals, for reports of communal egg-laying. In addition, we exhaustively searched all issues of regional herpetological journals that were not indexed in zoological databases or that were not available online, although acquiring regional, non-English language journals was not always possible. In total, our assembled database was gathered from 290 different sources, including 176 different scientific journals, 72 books or book chapters, 29 unpublished reports, and 13 unpublished theses. We also have included a number of reliable personal communications from herpetologists. Despite this, our database will undoubtedly underestimate the incidence of communal egg-laying in reptiles and amphibians. The results of our review are provided in a single table in the Supplementary Online Materials, hereafter referred to as the SO Table (available online at *The Quarterly Review of Biology* homepage, www.journals.uchicago.edu/QRB). The table includes the species, the type of communal egg-laying that occurs, and the reference(s) for each.

TAXONOMIC DISTRIBUTION OF COMMUNAL EGG-LAYING IN REPTILES AND AMPHIBIANS

We documented communal egg-laying in 481 species of reptiles and amphibians (SO Table), and our analysis indicates that communal egg-laying is much more common than generally recognized (see Graves and Duvall [1995] for a review in squamate reptiles). Our database also shows that communal egg-laying may be more common in reptiles ($N = 345$) than in amphibians ($N = 136$). Although the proportion of communally laying species is modest for each group (Table 1), the proportion of species known to lay communally may greatly underestimate the prevalence of communal egg-laying among those groups, as the eggs or nests are unknown in many species (Test and Heatwole

1962; Juterbock 1986; Shine 1991; Perry and Dmi'el 1994). Although the difficulty in locating nests hampers our ability to determine the actual frequency of communal egg-laying among species, we can better estimate this proportion by dividing the number of known communally egg-laying species by the total number of species, *excluding those for which eggs have not been found*. We conducted such a calculation for the three families of Australian lizards known to include multiple communally egg-laying species—Gekkonidae, Pygopodidae, and Scincidae—as gleaned from the Encyclopedia of Australian Reptiles database (Greer 2004). Proportions of these lizard families known to lay communally were 4–9%, but, when we exclude species for which nests are not known, these values rise dramatically to 73–100% (Table 2). For a breakdown of the prevalence of communal egg-laying within reptiles and amphibians, as well as a discussion of the factors (ecological, morphological, physiological) that contribute to the taxonomic distribution of this behavior, see the Supplementary Online Materials.

MACROEVOLUTION OF COMMUNAL EGG-LAYING IN LIZARDS

In order to gain a better understanding of those situations under which communal egg-laying might evolve, it is helpful to examine the macroevolution of this trait using a phylogenetically-based comparative study. Unfortunately, such a comparison is made difficult by our inability to confidently assign “no communal laying” to a large proportion of species in which the eggs or nests are unknown. Despite this limitation, it is feasible to track the evolution of communal egg-laying in a particular group (1) if the eggs or nests are known in several closely-related species, or (2) if higher-order comparisons are made (e.g., family level comparisons). The latter comparison has not been attempted, but Jockusch and Mahoney (1997) mapped the presence/absence of communal nesting in a small group of plethodontid salamanders. They concluded that the evolution of communal nesting was an old event in the history of the

TABLE 1
Family-level proportions of reptiles and amphibians known to lay communally

Taxa with known communal nesting	Number of species	Number of oviparous species	Number known to nest communally (% of oviparous)
Reptilia			
Sauria			
Agamidae	381	375	3 (>1%)
Anguillidae	112	34	1 (3%)
Chameleontidae	161	134	1 (1%)
Cordylidae	54	15	2 (13%)
Gekkonidae	1076	1057	129 (12%)
Gerrhosauridae	32	32	2 (6%)
Gymnophthalmidae	193	193	11 (6%)
Iguanidae	36	36	13 (36%)
Lacertidae	279	278	9 (3%)
Phrynosomatidae	125	125	5 (4%)
Polychrotidae	393	393	15 (4%)
Pygopodidae	36	36	4 (11%)
Scincidae	1305	~744	41 (6%)
Teiidae	121	121	7 (6%)
Tropiduridae	309	224	12 (5%)
Total lizards	4232	3422	255 (7%)
Serpentes			
Colubridae	1827	~1663	40 (2%)
Elapidae	138	137	6 (4%)
Hydrophiidae	177	53	2 (4%)
Leptotyphlopidae	93	93	3 (3%)
Pythonidae	74	35	1 (3%)
Total snakes	2309	1981	52 (3%)
Chelonia			
Carettochelydidae	1	1	1 (100%)
Cheloniidae	6	6	6 (100%)
Chelydridae	2	2	1 (50%)
Dermochelydidae	1	1	1 (100%)
Emydidae	41	41	10 (5%)
Geoemydidae	69	69	3 (4%)
Kinosternidae	25	25	2 (4%)
Podocnemididae	8	8	4 (38%)
Trionychidae	30	30	2 (7%)
Total turtles	183	183	30 (16%)
Crocodylia			
Alligatoridae	9	9	1 (11%)
Crocodylidae	13	13	4 (31%)
Gavialidae	1	1	1 (100%)
Total crocodilians	23	23	6 (26%)

continued

TABLE 1
(continued)

Taxa with known communal nesting	Number of species	Number of oviparous species	Number known to nest communally (% of oviparous)
Rynchocephalia			
Sphenodontidae	2	2	2 (100%)
Total tuataras	2	2	2 (100%)
Total reptiles	6747	5609	333 (6%)
Amphibia			
Anura			
Ascaphidae	1	1	1 (n/a)
Bufonidae	~455	~451	14 (3%)
Centrolenidae	~135	~135	1 (1%)
Dendrobatidae	~205	~205	1 (>1%)
Discoglossidae	10	10	2 (20%)
Hylidae	~835	~835	11 (1%)
Leptodactylidae	~122	~121	11 (9%)
Myobatrachidae	124	124	11 (9%)
Pelobatidae	11	11	3 (27%)
Ranidae	~600	~600	24 (4%)
Rhacophoridae	~300	~300	4 (1%)
Total frogs	2798	2794	83 (3%)
Caudata			
Ambystomatidae	30	30	7 (23%)
Cryptobranchidae	3	3	1 (33%)
Hynobiidae	43	43	8 (19%)
Plethodontidae	~360	~360	25 (7%)
Proteidae	6	6	1 (17%)
Ryacotritonidae	6	6	3 (50%)
Salamandridae	62	57	7 (12%)
Sirenidae	4	4	1 (25%)
Total salamanders	514	509	53 (10%)
Total amphibians	3312	3303	136 (4%)
Total species	10059	8912	481 (5%)

Data are gleaned from the table in the Online Supplementary Materials (available online at *The Quarterly Review of Biology* homepage, www.journals.uchicago.edu/QRB).

clade and that it has thus persisted under a variety of ecological conditions (see also Nussbaum 2003).

We used a well-accepted phylogeny of squamate reptiles (Townsend et al. 2004) as the basis for a simple comparative analysis of the evolution of communal egg-laying at the family level in lizards. We produced a conservative summary of phylogenetic relationships using their most

highly-resolved phylogeny (Figure 9b in Townsend et al. 2004), and recognized several missing iguanid families based on another published phylogeny (Schulte et al. 2003). We then mapped the presence or absence of communal egg-laying in each lizard family on the phylogeny (Figure 1). The clear result is that communal egg-laying is widely distributed among lizard families and appears to have evolved

TABLE 2
Prevalence of communal egg-laying among three Australian lizard families

Group (N)	Proportion known to lay communally (N)	Proportion known to lay communally, excluding species in which nests are unknown (N)
Gekkonidae (111)	9% (10)	100% (10)
Pygopodidae (38)	8% (3)	100% (3)
Scincidae (262)	4% (11)	73% (15)
Total (411)	6% (24)	86% (28)

Communal egg-laying is much more prevalent than previously recognized, as evident among three Australian lizard families. Proportions of species known to lay communally in each family range from 4–9%, but when species for which nests are not known are excluded, these values rise to 73–100%. N = number of species.

independently multiple times (Figure 1). This result persists regardless of the phylogeny used (see Townsend et al. 2004

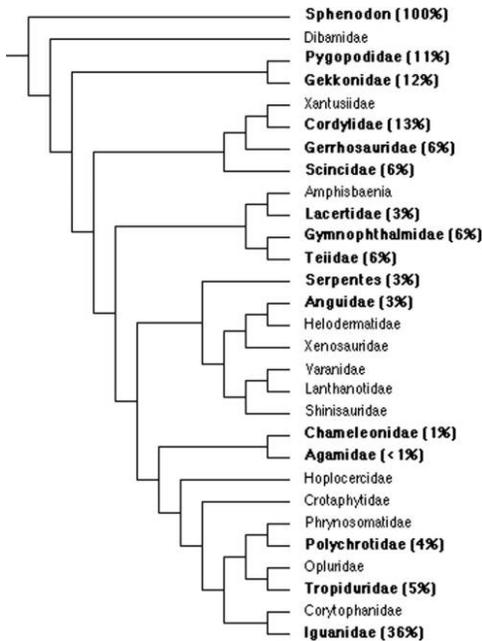


FIGURE 1. DISTRIBUTION OF COMMUNAL EGG-LAYING ACROSS LIZARD FAMILIES

The phylogeny is based mainly on the most highly-resolved squamate reptile tree presented in Figure 9b of Townsend et al. (2004). We also included several iguanid families that were missing from Townsend et al. (2004); their relationships are based on another published hypothesis (Schulte et al. 2003). Families that include species that display communal egg-laying are featured in bold typeface, and the known proportion of species that display this behavior is noted (see Table 1 for full details).

for various topologies). While it is virtually impossible to adequately reconstruct ancestral character states for these data because there is so much missing information, we can definitively ascertain that communal egg-laying is widespread across the phylogeny with multiple independent origins—and possibly reversals—of communal egg-laying (Figure 1). This is consistent with many of the hypotheses we present below.

HYPOTHESES FOR WHY REPTILES AND AMPHIBIANS LAY COMMUNALLY

There are two types of hypotheses that may explain communal egg-laying in reptiles and amphibians: “by-product” hypotheses, based on the scarcity of egg-laying sites or other factors causing coincidental aggregations of nesting mothers, and “adaptive” hypotheses, involving benefits to mothers, eggs, or hatchlings. We discuss these separately, as follows.

By-Product Hypotheses *Saturated Habitat Hypothesis*

The scarcity of suitable nest sites is commonly evoked as an explanation for why reptiles and amphibians lay communally (Rand 1967; Graves and Duvall 1995). This is a variation of the saturated habitat hypothesis offered to explain communal breeding in birds (Koford et al. 1986; Brown 1987). Indeed, communal egg-laying in other animals is sometimes attributed to patchy resources or few available nest sites (Michener 1974; Stamps 1980;

Danchin and Wagner 1997; Hayes 2000). That is, communal egg-laying may result from mutual attraction to restricted nest sites of superior quality, as several authors have suggested for reptiles (Graves and Duvall 1995; Pleguezuelos et al. 2004), and mothers may choose rare egg-laying sites based on attributes such as cover, structure, temperature, moisture, or, as in some amphibians, the presence of small breeding pools (e.g., Roberts 1994).

Remarkably, only one study has tested this hypothesis in reptiles or amphibians in nature, despite the relative ease of quantifying the aforementioned attributes between the communal egg-laying sites and potential sites accessible to mothers (Graves and Duvall 1995). Harris et al. (1995) manipulated the population density of female salamanders and found that it had no effect on the frequency of communal nesting, noting that communal nesting was common at low densities where nesting habitat saturation was unlikely. However, two additional lines of evidence indicate that, in many cases, habitat saturation cannot explain communal egg-laying in reptiles and amphibians. First, it is not uncommon for communal egg-laying sites to be surrounded by potential sites with identical or similar attributes (Rand and Dugan 1983; Magnusson and Lima 1984; Mora 1989; Burger and Zappalorti 1991; Brown and Duffey 1992; Hayes et al. 2004; Doody 2006), and, relatedly, the eggs laid are often spatially clumped under or within the cover object, despite apparent homogeneous conditions under the object. Radder and Shine (2007) predicted that if nest sites were limited, more communal clutches would be found under larger cover objects. They found no correlation between the size of the cover object and the number of lizard eggs beneath it, and they cited this as evidence against the saturated habitat hypothesis. Second, experiments were conducted in both the laboratory and the field in which communal egg-laying was elicited in snakes, lizards, and frogs. In one laboratory experiment, snake mothers nested communally in an enclosure with abundant and equivalent

nest sites (Plummer 1981), while in another experiment, snakes preferentially nested in artificial nest sites that contained conspecific eggshells over sites with no eggshells (Brown and Shine 1995). Similarly, lizards preferred to nest with dummy eggs (eggshells filled with cotton wool) rather than with controls (Radder and Shine 2007). In the field, Howard (1980) stimulated communal egg-laying in a frog by introducing clutches to a suboptimal area of a breeding pond (but see also Seale 1982).

Sexual Selection Hypothesis

Communal egg-laying could be an artifact of mate choice in animals that mate at the oviposition site. Polygamy is common in amphibians, and attending males are often associated with egg clutches of several females (Duellman and Trueb 1986). In such cases, communal clutches may be directly due to a female's choice of males, rather than her choice of oviposition site. In an exceptional example, males of the frog genus *Alytes* simultaneously carry up to four clutches on their backs, although the number of females involved is unknown (Marquez and Verrell 1991; Reading and Clarke 1988). In a sense, males become the limiting resource, and thus, theoretically, there is no direct benefit of communal egg-laying. More generally, data are needed on whether or not the communal oviposition site is chosen by the mother or the male. In at least one species, mothers carry amplexing males to the growing communal mass (Howard 1980; Seale 1982).

Relatedly, in a hypothesis applicable only to frogs (due to external fertilization), Herreid and Kinney (1967) suggested that fertilization success may be increased if communal egg masses are associated with intensive mating and, thus, surplus sperm. Indeed, multiple paternity in a communally egg-laying ranid frog was attributed to free-swimming sperm in the water produced by non-amplectant males (Laurila and Seppa 1998). However, this may have been the result of "pirate" males clasping and fertilizing egg masses already fertilized

by amplexed males rather than surplus sperm (Vieites et al. 2004).

Artifact of Aggregation for Other Reasons

Communal egg-laying could be an artifact of other behaviors. For example, it may result from social behavior among mothers, as, in some cases, social interactions occur at communal egg-laying sites (Graves and Duvall 1995). Although social interactions are generally less complex in reptiles and amphibians than in other tetrapods (Wilson 1975), they nevertheless occur in many species (Brattstrom 1974). In particular, social aggregations occur in several species of geckos (Greenberg 1943; Cooper et al. 1985; Kearney et al. 2001; Lopez-Ortiz and Lewis 2002), which, as a group, possess the highest incidence of communal egg-laying among lizards (SO Table; Table 1). Indeed, at least one species of gecko is known to communally nest (SO Table) (Kearney et al. 2001). In another example, gravid iguanas exhibit territorial displays in nesting areas, but not in nearby non-nesting aggregations (Carpenter 1966; Rand 1968; Rand and Rand 1976; Rand and Rand 1978).

The kin selection hypothesis suggests that relatives contribute to communal clutches (Tallamy 1985). Specifically, mothers from the same maternal lineage are expected to gravitate to the same egg-laying area, causing an aggregation of related females. The resulting communal nesting is not an adaptation in itself, because mothers may not directly benefit from laying with conspecifics. Graves and Duvall (1995) suggested that communal egg-laying in squamate reptiles may result from perennial nesting due to natal homing (Rand and Dugan 1983; Mora 1989; Burger and Zappalorti 1992). No study has addressed this possibility in reptiles or amphibians, but there is evidence for such relatedness in birds (Koenig and Stacey 1990). The behavior could be particularly relevant when there are multiple brooders (Tallamy 1985), but multiple brooders are rare in reptiles and amphibians (Harris et al. 1995; but see McDiarmid and Gorzula 1989); however, molecular data suggest

that natal homing produces aggregates of closely-related nesting females in several turtle species (Meylan et al. 1990; Allard et al. 1994; Freedberg et al. 2005).

Adaptive Hypotheses

Animals often make critical decisions by copying the choices of conspecifics (Pruett-Jones 1992; Danchin and Wagner 1997), and social acquisition of information has been well-documented in a variety of animal systems (Giraldeau 1997; Galef and Giraldeau 2001). These non-independent choices are believed to benefit "copiers" or "freeloaders" by offering a savings in time, energy expenditure, or survival, relative to independent choices (Giraldeau et al. 2002). Assuming these benefits outweigh associated costs, we might expect to find copying behavior in populations or species where it is free to evolve. A mother with the task of searching for a place to lay her eggs could realize such benefits by copying the oviposition site choice of conspecifics. Alternatively, her offspring could benefit.

Attack Abatement Hypothesis

Attack abatement (*sensu* Turner and Pitcher 1986) has two theoretical components: an encounter probability and a dilution effect (Wrona and Dixon 1991). For communal egg-laying, the encounter probability predicts that a predator is less likely to find a single group of many eggs than many scattered smaller groups of eggs. By laying with conspecifics, the dilution effect predicts that the number of eggs in a site would increase, potentially reducing the probability of predation of each mother, egg, or neonate through predator saturation or satiation (Robinson and Bider 1988; Eckrich and Owens 1995; Harris et al. 1995; Spencer 2002; Doody et al. 2003a). Graves and Duvall (1995) pointed out that this would be particularly plausible if temporal synchrony of nesting occurs, as is known in communally nesting iguanas (Wiewandt 1982; see also McMullan 2000 for evidence in dragonflies). Other authors have suggested that such benefits may be realized in reptile mothers

(Wiewandt 1982; Burger and Zappalorti 1992), eggs (Fitch 1954; Shine 1979; but see Robinson and Bider 1988) or neonates (Burghardt 1977; Burghardt et al. 1977).

Evidence for these benefits in reptiles and amphibians is scarce. In the only published study comparing predation rates between communal and solitary reptile nests, Brown and Duffy (1992) found no differences in predation rates or hatching success in a gecko. However, more predatory leeches were found on solitary egg masses than in communal masses of a frog (Hakansson and Loman 2004), possibly indicating a dilution effect. Carreno and Harris (1998) proposed that nest care in a salamander was consistent with the predator dilution hypothesis, and predators, in this case, included beetles, centipedes, and newts. More generally, few studies have tested the influence of spatial and temporal distributions of nests on the probability of predation in reptiles (reviewed in Burke et al. 1998; Doody et al. 2003b), and still fewer have found an effect (but see Drummond 1983; Robinson and Bider 1988).

The implication of predator satiation as an adaptive mechanism for communal egg-laying would depend on the relative sizes of the eggs and predators. Large predators of lizard, snake, turtle, and frog eggs are known to consume an entire clutch (Carter 1992; Donnelly and Guyer 1994; Warkentin 2000; Doody et al. 2003b) and would be difficult to satiate. Medium-sized predators are known to take partial clutches in lizards and frogs (e.g., Bogert 1940; Hayes 1983) and thus could be satiated by communal efforts. However, in theory, the predator could return in a few days to consume the remainder of the eggs, at least in species in which development is prolonged. Furthermore, in many animals (i.e., turtles), consumption of just one egg can doom the entire clutch, since the integrity of the nest cavity would be destroyed. Perhaps even better candidates for predator dilution are the invertebrates, which generally take fewer eggs (Villa et al. 1982; Downie et al. 1995) and are less likely to damage the nest cavity structure. Invertebrate predators of reptile eggs include ants, snails, and beetles (Andrews 1982;

1988; Allen et al. 1997; Blouin-Demers and Weatherhead 2000; Smith et al. 2007). Amphibian eggs may attract a larger suite of invertebrate predators, including ants, spiders, beetles, crickets, wasps, fly larvae, and leeches (Bokermann 1957; Howard 1978; Hayes 1983; Duellman and Trueb 1986; Barreto and Andrade 1995; Warkentin 2000; Giaretta and Menin 2004; Hakansson and Loman 2004). Finally, any advantages of communal nesting with respect to predation would be influenced by the palatability of eggs. Eggs of some frogs and salamanders, for instance, are unpalatable to invertebrate and vertebrate predators (Hess and Harris 2000).

Maternal Benefits Hypothesis

Communal egg-laying may provide maternal benefits, such as a savings in energy and time or increasing the likelihood of survival. First, by adding their eggs to those of conspecifics, mothers could reduce energetic costs associated with searching for an egg-laying site, assessing potential egg-laying site characteristics, and, in some cases, carrying out nest excavation. Experimental evidence for such benefits is limited, but it has been demonstrated in communally laying insects that save time and energy by ovipositing into host fruits with conspecific bore holes, despite the potential costs to offspring in increased competition and, consequently, survival (Papaj et al. 1992; Lalonde and Mangel 1994). In extreme cases, the time and energy involved in solitary nest excavation can be prohibitive, as in some bee species (Danforth 1991). Nesting migrations can be substantial in reptiles such as sea turtles or some iguanas (Bjorndal 1982; reviewed in Hayes et al. 2004), thereby placing considerable energetic strains on those animals that may ultimately lead to selection for minimizing energy expenditure once the nesting areas are reached (Bjorndal 1982; Bull and Shine 1979; Werner 1983; but see Congdon and Gatten 1989). At least some species of iguanas, tuataras, and snakes take several days to complete nesting (Rand 1968; Hayes et al. 2004; N. Nelson, personal communication; Burger and Zap-

palorti 1992). Soils are extremely hard or compact at some nesting sites, and, as a result, nesting burrow excavation requires considerable time and energy. Mothers of these species are known to deposit their eggs in the chambers of conspecifics (references above), and may save considerable energy and time, or ensure their survival, by doing so (Bock and Rand 1989; Mora 1989; Burger and Zappalorti 1991; Rand and Dugan 1983; Wiewandt 1982). The commonness of mothers excavating previous nesting burrows to save on excavation costs at communal nest sites is manifested in vigorous nest defense against conspecifics in some iguana species and in tuataras (Rauch 1988; N. Nelson, unpublished data).

Second, in addition to energetic costs, these tasks could involve allocating considerable time that could otherwise be spent foraging or performing other important activities such as feeding or thermoregulation. Third, communal egg-laying may be the result of predator avoidance if the landscape of predation is patchy. In at least some animal systems, mothers are especially vulnerable to predation during egg-laying. Dragonflies, for instance, have been known to reduce their vulnerability to predation by ovipositing communally in frog-free areas of ponds (McMillan 2000). Evidence is lacking in reptiles and amphibians (although frogs preferentially oviposited in predator-free experimental ponds [Resitaris and Wilbur 1989]), but communal egg-laying in complex burrow systems may allow lizard mothers to reduce their accessibility to predators during nesting (Rand and Dugan 1983).

Reproductive Success-Based Hypothesis

Mothers may use specific fitness components as cues for communal egg-laying (Danchin and Wagner 1997). A number of reports of communal egg-laying in reptiles included evidence of the repeated use of a nest site, either over the course of years or among clutches within a year (Werner 1986). Our review indicated that over one-third of the papers on reptile communal egg-laying described eggshells in the egg-laying sites from previous clutches or years.

In the laboratory, a snake preferentially oviposited in sites with conspecific eggshells over shell-free sites, prompting the authors to invoke successful hatching as a cue for nesting mothers (Brown and Shine 2005). However, it is inconclusive whether mothers evaluated eggshells as evidence of successful hatching, or simply as evidence that conspecific egg-laying had occurred. Experiments using both hatched and unhatched eggshells as stimuli are needed.

Egg Insulation Hypothesis

Communal egg-laying may confer a thermal advantage in ectotherms, and this has been used to explain the evolution of this behavior in some temperate aquatic frogs. In several ranid frogs from North America, Europe, and Asia (SO Table), up to hundreds of egg masses are deposited into communal clusters in breeding ponds. In three frog species, eggs in the centre of a communal mass averaged temperatures 1–7°C warmer than those of either solitary egg masses or egg masses on the periphery of the communal mass or surrounding water (Guyétant 1966; Howard 1980; Waldman 1982; Waldman and Ryan 1983; Hakansson and Loman 2004). Resulting increased temperatures are said to be adaptive in preventing freezing and in reducing incubation times (Seale 1982; Waldman 1982; Waldman and Ryan 1983). In one species, developmental time was reduced by 1–3 days in the centre of communal masses relative to solitary masses (Hakansson and Loman 2004). A key biogeographical pattern underlying this hypothesis is that these species breed either in cold climates or during the winter in milder climates (Caldwell 1986; Doody and Young 1995). In reptiles, Blouin-Demers et al. (2004) suggested that communal nesting incurred a thermal advantage to embryos in a population of snakes < 20 km from a cold climate range margin. Communal egg masses were nearly 5°C warmer on average than isolated masses, and the authors used incubation experiments to suggest that the warmer temperatures offered by communal masses would result in faster hatching and longer, faster, and less

aggressive neonates than those from isolated nests. In contrast, the thermal environment did not differ between communal and isolated nests in a lizard at a cold climate extreme (Radder and Shine 2007). However, in the laboratory, eggs in groups took up less water, resulting in hatchlings that were also larger and faster.

Contrary to predictions of this hypothesis, many tropical species of both amphibians and reptiles exhibit communal egg-laying behavior (SO Table). Although this number is lower than that of temperate species, such a pattern would be expected due to the "boreal bias" (Platnick 1991). An analysis is needed of the breakdown of the incidence of communal egg-layers across different climates, using only species for which the eggs in nature are known. However, in aquatic amphibians, such analysis would need to consider the confounding temperature constraint on oxygen transport in egg aggregations (Seymour 1995; Strathmann and Strathmann 1995).

A related hypothesis, suggested for and possibly restricted to amphibian eggs, involves resistance to desiccation rather than extreme temperatures (Ryan 1985). Frog egg masses centrally located within communal masses withstood up to 14 days of terrestrial stranding (Forester and Lykens 1988; but see Paton et al. 2003). In support of this, experimental communal frog nests desiccated more slowly than isolated nests, and embryos survived longer as a consequence (Zina 2006). Finally, communal egg masses may insulate against environmental factors other than temperature and moisture. Karn (1992) found evidence that large numbers of communal egg masses modify the local chemical environment of developing eggs, thus ameliorating the effects of toxic bog water (low pH).

Other Adaptive Hypotheses

A few other adaptive hypotheses for communal egg-laying have been offered, but these are restricted to animals exhibiting parental care, and, thus, have limited applicability with regard to our review (<2% of the species in our review are known to brood

their eggs). These include the aggressive usurpation (AU) hypothesis, the intraspecific brood parasitism (IBP) hypothesis, and the multiple defenders (MD) hypothesis. The AU hypothesis involves later-nesting mothers displacing earlier-nesting mothers, thus allowing them to secure a nest site and possibly eat the conspecific's eggs (Vehrencamp 1978; Koford et al. 1990). The IBP hypothesis involves a mother laying her eggs with those of a conspecific and then deserting them, leaving the indiscriminant conspecific mother to brood (reviewed in Zink 2000; 2001; 2005). The MD hypothesis posits that communal egg-laying may have evolved as a result of increased nest defense from predators in species that brood their eggs (McGowan and Woolfenden 1989; Pilastro 1992). These three hypotheses were proposed and later rejected as explanations for communal egg-laying in a brooding salamander (Harris and Gill 1980; Harris et al. 1995), as communal egg-laying in that species may be maintained by the transmission of antifungal bacteria. Compared to solitary nests, communal nests were more likely to be associated with cutaneous antifungal bacteria, and experienced higher embryonic survival and lower nest failure accordingly (Banning et al. 2008; Harris 2008).

Mixed Models and Evaluation of the Evidence

Adaptive hypotheses for communal egg-laying involve conspecific cueing (Danchin and Wagner 1997), and, as such, need not reflect a shortage or patchiness of egg-laying sites. However, longer-term scarcity of nest sites would, in theory, increase the average cost of searching for an egg-laying site, which could select for communal egg-laying. Thus, demonstrating egg-laying site rarity does not necessarily undermine adaptive explanations, and limited nest sites could favor the maternal benefits hypothesis. Moreover, the adaptive models are not mutually exclusive of one another.

Can any of these hypotheses serve as a general explanation for communal egg-laying in reptiles and amphibians? No

study has comprehensively attempted to determine the significance of communal egg-laying among these groups of animals (but see Harris et al. 1995 for a thorough attempt at determining the causes in a salamander). The mostly anecdotal evidence reviewed here strongly suggests that different forces may be driving the evolution and maintenance of communal egg-laying in different taxa. Regardless, the habitat saturation hypothesis is inadequate to explain communal egg-laying in many cases, and conspecific cueing in both the laboratory and the field offers strong indirect evidence for an adaptive function. Nevertheless, experiments are needed to conclusively demonstrate that communal egg-laying is not due to limited nest sites and to determine the relative explanatory value of the adaptive models.

AN ESS MATERNAL BENEFITS MODEL FOR
THE FREQUENCY OF COMMUNAL EGG-
LAYING IN ANIMALS WITHOUT PARENTAL
CARE

Any adaptive model for communal egg-laying needs to be able to explain why solitary clutches and communal clutches generally co-exist in a given population. For example, communal egg-laying apparently occurs only at high densities in some species (e.g., Knapp and Hudson 2004; but see Harris et al. 1995), and so the behavior is likely to be context-dependent in these groups (see Ward and Kukuk 1998 for an example in invertebrates with parental care). While we have identified several scenarios that favor communal egg-laying, the maternal benefits model, in particular, is likely to apply to a wide range of taxa. In these systems, the incidence of communal egg-laying is probably determined by factors dictating the cost-benefits associated with choosing an egg-laying site versus finding an egg-laying site of a conspecific (freeloading). It follows that, in many cases, finding the clutch of a conspecific might either be unlikely or energetically costly, especially at low population densities. How would communal egg-laying persist in populations with low densities in

which the chances of a mother discovering the nest of a conspecific are limited?

The Model

We consider a population with two ovipositing strategies. "Choosers" (C) physically search for egg-laying sites and excavate nests, while "freeloaders" (F) deposit their eggs in nests constructed by choosers. We assume that freeloaders is a purely commensal behavior; choosers suffer no fitness detriment by being copied. Let l be the fitness gained through each clutch of offspring. Choosers also suffer a fitness cost, k , associated with searching for a suitable egg-laying site (and possibly with carrying out nest construction) that freeloaders do not. Several factors contribute to k , including predation risks and energy expenditure associated with assessing incubation conditions and constructing nests. Freeloading females do not suffer these costs. Generally, females are predicted to benefit from nesting successfully despite these costs, and thus $k < l$.

If freeloaders successfully locate an existing nest, the fitness change is l (as opposed to $l - k$ for choosers), since freeloaders do not suffer the costs associated with assessing incubation conditions. In the absence of finding a chooser's conspecific egg clutch, however, freeloaders will eventually search out their own egg-laying sites (and possibly construct their own nests) and will suffer the cost of finding an egg-laying site, k . In addition, because freeloaders will have already spent time fruitlessly searching for conspecific clutches, they will suffer an additional fitness cost, s , associated with compromised nest quality resulting from having less time and energy to utilize, as compared to choosers, in finding a suitable egg-laying site and constructing a nest. Our approach is similar to that of game theoretical approaches to modeling mate choice behavior (Pruett-Jones 1992).

Let p equal the proportion of choosers in the population, and let $(1 - p)$ equal the proportion of freeloaders. Furthermore, the probability that a freeloader will find a conspecific egg clutch will be depen-

dent upon the frequency of choosers. For the sake of simplification, we will assume for now that the probability of finding a conspecific egg clutch is equal to p , the proportion of choosers in the population. Thus, if the population consists of 60% choosers, each freeloader will have a 60% chance of finding a conspecific clutch and a 40% chance of being forced to find their own suitable egg-laying site (and possibly construct a nest).

The total fitness, W , of choosers will be equal to $W(C) = l - k$, while the fitness of freeloaders will be equal to $W(F) = p^*l + (1 - p)(l - k - s)$. At equilibrium, the fitness of the two strategies must be equal (Maynard Smith 1982). Thus:

$$l - k = p^*l + (1 - p)(l - k - s) \quad (1)$$

which simplifies to:

$$p = s / (s + k). \quad (2)$$

Because s and k are both bound by 0 and 1, we can deduce that $0 < p < 1$ and, consequently, $0 < (1 - p) < 1$. Therefore, at equilibrium, the freeload and choosing strategies will co-exist as long as there are non-zero costs associated with finding or constructing a suitable egg-laying site and with failed attempts at freeload. Unless the frequency of choosers is very low, it is unlikely that all chooser nests will be discovered by freeload females, and, therefore, some nests will remain solitary while others will become communal.

To elucidate the finding in (2) even further, we can suppose that instead of suffering a cost, s , females that attempt to freeload and cannot locate a conspecific egg clutch will not lay at all. Our equation then becomes:

$$l - k = p^*l + (1 - p)(0) \quad (3)$$

which simplifies to:

$$p = (l - k) / l. \quad (4)$$

Because $l > k$ and both must be greater than 0, we can again see that $0 < p < 1$ and, consequently, $0 < (1 - p) < 1$.

This qualitative result—that a polymorphism of choosing and freeload will remain in the population at equilibrium—is

robust to our simplifying assumption that the probability of finding a conspecific egg clutch is exactly equal to p , the proportion of choosers in the population. If the probability of finding a chooser's nest is greater than p , such that we can say it is p^r , where $0 < r < 1$, and therefore the probability of failing to find a nest is $(1 - p^r)$, the equilibrium proportion of nesters is now equal to

$$p = (s / (s + k))^{1/r}. \quad (5)$$

Given that $(1 > r > 0)$, p must still be bound by 0 and 1 at equilibrium, and both strategies will coexist, with freeload being more common than in (2).

We can alternatively assume that the probability of finding a conspecific nest is lower than p . If the probability of a freeloader finding a conspecific nest is again p^r , where r is now greater than 1, both strategies will still be maintained at some level in the population, although freeload will be rarer than in (2).

Although non-equilibrium conditions may also affect the frequency of these two strategies, we can see that, outside of such disturbances, there are plausible conditions that lead to the stable coexistence of these strategies. It is interesting to ask why the coexistence of these strategies is not more common. In short, any costs associated with attempting to freeload may prevent the invasion of a freeload strategy. Such costs can be incorporated into the model by adding a fitness penalty—an additional negative value—to $W(F)$, and doing so can allow choosing to spread to fixation, depending on the size of the penalty. We outline the nature of these costs in the next section.

COSTS OF COMMUNAL EGG-LAYING

The seemingly ubiquitous occurrence of non-communal clutches in communally laying populations suggests that the latter is likely to incur costs as well as benefits. In the simplest example, if nest densities are low in communal layers (i.e., due to low population density), the costs associated with finding the eggs of conspecifics may be higher than those associated with find-

ing one's own egg-laying site, thus favoring more solitary nesters (as quantified above). In colonial nesters with high nesting densities, another cost is the destruction of eggs by conspecific females (Graves and Duvall 1995). For example, Alonso et al. (2002) showed that nearly 20% of crocodile nests were destroyed by conspecific nesting females over an 11 year period. Also, excavated reptile eggs usually desiccate, or they are eaten by the excavating mother, conspecifics, or other animals (e.g., Sexton 1975).

A cost associated with group living is increased disease transmission (Alexander 1974; Brown and Brown 1996), and this could be extended to egg aggregations. For example, frogs that oviposit communally may suffer higher egg mortality caused by fungal infection (Blaustein et al. 1994; Kiesecker and Blaustein 1997; but see Banning et al. 2008). Similarly, parasitoid beetles appear to exploit snake eggs in communal nests more readily than eggs in solitary nests (Blouin-Demers et al. 2004). Another potential cost of communal egg-laying is that concentrations of adults, eggs, or mothers could attract predators (Christian and Tracy 1981; Graves and Duvall 1995)—an opposite supposition to the predator dilution hypothesis. Finally, Marco et al. (2004) discussed the possibility that eggs in communal lizard nests experience increased competition for soil water, relative to solitary egg nests (but see Blouin-Demers et al. 2004; Radder and Shine 2007).

SUMMARY AND RECOMMENDATIONS FOR FURTHER RESEARCH

Our analysis of the prevalence of communal egg-laying (SO section) has two important implications. First, it indicates that communal egg-laying in reptiles and amphibians is much more common than previously recognized. For example, in an exceptional treatment of the biology of lizards, Pianka and Vitt (2003) scarcely mention communal egg-laying and generally dismiss the behavior as an artifact of a shortage of nest sites. Second, the present review highlights our inadequate knowl-

edge of the nests and/or eggs of reptiles. For instance, the eggs or nests are known in only 7% of Australian lizards of the three families that commonly lay communally ($N = 411$ oviparous spp.) (Greer 2004). The extent of this knowledge for Australian lizards is probably similar to that for reptile eggs on other continents, particularly South America, Africa, and Asia, where the reproductive habits of reptiles are poorly known. This is in stark contrast to other vertebrates such as birds, for which complete field guides to the eggs and nests are available for several continents (Harrison 1975; Beruldsen 1980; Baicich and Harrison 1997). The eggs of amphibians are generally better known because calling males tend to draw observers to breeding sites (Duellman and Trueb 1986).

From a broader perspective, our review informs both behavioral and evolutionary ecology. For example, a considerable body of theory predicts that because conspecifics are competitors, individual fitness should decrease with increasing density (Rosenzweig 1991; Sutherland 1996), and there is indeed evidence for conspecific avoidance at oviposition sites (Resitarits and Wilbur 1989; Crump 1991). However, recent research suggests the opposite: conspecific attraction has been experimentally demonstrated in ovipositing animals (Downie et al. 2001; Brown and Shine 2005; Rudolf and Rodel 2005; Radder and Shine 2007). Conspecific attraction and conspecific cueing are not new ideas (e.g., see Stamps 1988). However, our review, along with these experimental studies, indicates that conspecific attraction can be adaptive for ovipositing mothers, and thus its benefits can offset disadvantages incurred by offspring (e.g., competition). We hope our review will stimulate more research in this fertile area. The relatively simple systems typical of most communally laying reptiles and amphibians can facilitate advances in our understanding of egg aggregations by bringing nest site choice and its associated costs and benefits into sharp focus. In this way, these organisms provide a means for narrowing the gap between evolutionary theory and the supporting empirical data by

offering ideal systems for understanding both fundamental adaptive advantages for animal egg aggregations and their attendant behavioral mechanisms, as well as contributing to a better understanding of conspecific attraction in animals.

How should future research into communal egg-laying proceed? What direction should we follow in further exploring this behavior? Although we argued above that the saturated habitat hypothesis cannot, in many cases, explain communal egg-laying, it may be the most parsimonious explanation for why a particular species lays communally, and it should therefore be investigated. The great number of species known to lay communally may simply reflect concentrations of available or successful nest sites. Support for this hypothesis would include demonstrating that the environment (i.e., temperature, moisture) encompassing the eggs does not exist immediately beyond them or in nearby areas accessible by nesting mothers. Focal observations of the movements associated with nesting, in conjunction with the above microhabitat analysis, would offer a more direct test. In another approach, the successful elicitation of communal egg-laying using eggs or eggshells as stimuli would disprove the saturated habitat hypothesis (Howard 1980; Plummer 1981; Brown and Shine 2005; Radder and Shine 2007).

An appropriate framework for investigating the adaptive value of communal egg-laying would involve quantifying the associated costs and benefits to both mothers and offspring. Parent-offspring conflict (*sensu* Hamilton 1964; Trivers 1974) could even occur in populations of communally laying species when the payoff for mothers (a savings of time and energy or increased likelihood of survival) offsets or exceeds the costs incurred by the offspring (e.g., competition, survival) (Takasu and Hirose 1992; Lalonde and Mangel 1994). Using this framework, we would predict communal egg-laying to occur in species or populations with relatively high costs to ovipositing mothers, compared to those incurred by their offspring. Thus, quantifying survival- and fitness-related traits in mothers and off-

spring could elucidate potential factors responsible for the evolution and maintenance of communal egg-laying (see also Harris 2008).

The egg-laying system of lizards is ideal for testing adaptive hypotheses for communal nesting in both the laboratory and in the field. First, in addition to the general lack of parental care exhibited by these animals, we note that, in reptiles, mating is generally uncoupled from the oviposition site. Second, the cue for communal egg-laying is likely to be the presence of eggs/eggshells, and these are often easily manipulated. Pheromones could also play a role in conspecific cueing, and these are also readily manipulated (see Papaj et al. 1992 for an example in insects). Maintaining a breeding colony of small lizards, such as skinks or geckos, is also straightforward. Manipulations in laboratory or field enclosures could determine: (1) whether conspecific cueing is occurring, and thus whether communal egg-laying is adaptive; (2) the influence of the availability of egg-laying sites on the propensity to lay communally; (3) the relative cues offered by eggs vs. eggshells (i.e., do eggshells signal nest sites of superior quality because eggs hatched successfully there? [Brown and Shine 2005]); (4) the existence of a dilution effect; (5) the relative amount of time and energy expended by communal layers vs. solitary layers; (6) the extent to which mothers would trade-off nest site quality to achieve communal nesting, given the apparent benefits; (7) the role of experience in the propensity to lay communally; (8) the influence of the energetic state of mothers on their propensity to lay communally (Harris 2008); (9) whether natal homing is occurring; and (10) behavior associated with communal egg-laying (e.g., movements and social interactions).

Field studies would also be useful in explaining communal egg-laying. For example, the costs of nesting are generally not known for reptiles and amphibians (but see Werner 1983; Congdon and Gatten 1989). What are the energetic and time costs associated with migration to an egg-laying site (Werner 1983; Congdon and

Gatten 1989; Burghardt 2004), assessment of egg-laying sites, and nest excavation (Wiewandt 1982)? How do these costs differ between communal and solitary layers? Studies of the relative proportion of communal vs. solitary layers would be particularly useful in species in which eggs are more easily located, especially in a comparative context. For instance, comparison of survival and other costs between two populations with differing proportions of communal layers might elucidate ultimate factors underpinning those proportions. Another potentially fruitful area of research would be the testing of the predator dilution hypothesis. Would a predator that is satiated by eating part of a communal clutch not return to consume the rest of the nest later? Identifying key egg predators could be invaluable in determining the proximate and ultimate causes of communal egg-laying in reptiles and amphibians.

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REFERENCES

- Allard M. W., Miyamoto M. M., Bjorndal K. A., Bolten A. B., Bowen B. W. 1994. Support for natal homing in green turtles from mitochondrial DNA sequences. *Copeia* 1994:34–41.
- Allee W. C. 1927. Animal aggregation. *Quarterly Review of Biology* 2:367–398.
- Allen C. R., Rice K. G., Wojcik D. P., Percival H. F. 1997. Effect of red imported fire ant envenomization on neonatal American alligators. *Journal of Herpetology* 31:318–321.
- Alexander R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Alonso M., Soberón R. R., Ramos R., Thorbjarnarson J. 2002. Mortality of eggs of *Crocodylus acutus* associated with the conduct of females in R. F. Monte Cabaniguán, Cuba. Poster presented at the 16th Working Meeting of the Crocodile Specialist Group SSS/IUCN, 7–10 October 2002, in Gainesville, FL.
- Andrade D. V., Nascimento L. B., Abe A. S. 2006. Habits hidden underground: a review on the reproduction of the *Amphisbaenia* with notes on four neotropical species. *Amphibia-Reptilia* 27(2): 207–217.
- Andrews R. M. 1982. Spatial variation in the egg mortality of the lizard *Anolis limifrons*. *Herpetologica* 38: 165–171.
- Andrews R. M. 1988. Demographic correlates of variable egg survival for a tropical lizard. *Oecologia* 76(3):376–382.
- Baichich P. J., Harrison J. O. 1997. *A Guide to the Nests, Eggs, and Nestlings of North American Birds*. Princeton (NJ): Princeton University Press.
- Banning J. L., Weddle A. L., Wahl G. W., Simon M. A., Lauer A., Walters R. L., Harris R. N. 2008. Antifungal skin bacteria, embryonic survival, and communal nesting in four-toed salamanders *Hemidactylium scutatum*. *Oecologia* 156(2):423–429.
- Barreto L., Andrade G. V. 1995. Aspects of the reproductive biology of *Physalaemus cuvieri* (Anura: Leptodactylidae) in northeastern Brazil. *Amphibia-Reptilia* 16(1):67–76.
- Beruldsen G. 1980. *A Field Guide to Nests and Eggs of Australian Birds*. Adelaide (Australia): Rigby.
- Birchard G. F. 2004. Effects of incubation temperature. Pages 103–123 in *Reptilian Incubation: Environment, Evolution, and Behavior*, edited by D. C. Deeming. Nottingham (UK): Nottingham University Press.
- Bjorndal K. A. 1982. The consequences of herbivory for the life history pattern of the Caribbean green turtle, *Chelonia mydas*. Pages 111–116 in *Biology and Conservation of Sea Turtles*, edited by K. A. Bjorndal. Washington (DC): Smithsonian Institution Press.
- Blaustein A. R., Hokit D. G., O'Hara R. K., Holt R. A.

1994. Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. *Biological Conservation* 67(3):251–254.
- Blouin-Demers G., Weatherhead P. J. 2000. A novel association between a beetle and a snake: parasitism of *Elaphe obsoleta* by *Nicrophorus pustulatus*. *Ecology* 7:395–397.
- Blouin-Demers G. P., Weatherhead J., Row J. R. 2004. Phenotypic consequences of nest-site selection in black rat snakes (*Elaphe obsoleta*). *Canadian Journal of Zoology* 82:449–456.
- Bock B. C., Rand A. S. 1989. Factors influencing nesting synchrony and hatching success at a green iguana nesting aggregation in Panama. *Copeia* 4:978–986.
- Bogert C. M. 1940. Herpetological results of the Vernay Angola Expedition with notes on African reptiles in other collections. Part I: Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History* 77:1–107.
- Bokermann W. C. A. 1957. Frog eggs parasitized by dipterous larvae. *Herpetologica* 13:231–232.
- Brattstrom B. H. 1974. The evolution of reptilian social behavior. *American Zoologist* 14(1):35–49.
- Brown C. R., Brown M. B. 1996. *Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior*. Chicago (IL): University of Chicago Press.
- Brown G. P., Shine R. 2005. Nesting snakes (*Tropidonophis mairii*, Colubridae) selectively oviposit in sites that provide evidence of previous successful hatching. *Canadian Journal of Zoology* 83(8):1134–1137.
- Brown J. L. 1987. *Helping and Communal Breeding in Birds*. Princeton (NJ): Princeton University Press.
- Brown S. G., Duffy P. K. 1992. The effects of egg-laying site, temperature, and salt water on incubation time and hatching success in the gecko *Lepidodactylus lugubris*. *Journal of Herpetology* 26(4):510–513.
- Bull J. J., Shine R. 1979. Iteroparous animals that skip opportunities for reproduction. *American Naturalist* 114:296–303.
- Burger J., Zappalorti R. T. 1991. Nesting behavior of pine snakes (*Pituophis m. melanoleucus*) in the New Jersey pine barrens. *Journal of Herpetology* 25(2):152–160.
- Burger J., Zappalorti R. T. 1992. Philopatry and nesting phenology of pine snakes *Pituophis melanoleucus* in the New Jersey pine barrens. *Behavioral Ecology and Sociobiology* 30(5):331–336.
- Burghardt G. M. 1977. Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. *American Zoologist* 17:177–190.
- Burghardt G. M. 2004. Iguana research: looking back and looking forward. Pages 1–12 in *Iguanas: Biology and Conservation*, edited by A. C. Alberts et al. Berkeley (CA): University of California Press.
- Burghardt G. M., Greene H. W., Rand A. S. 1977. Social behavior in hatchling green iguanas: life at a reptile rookery. *Science* 195(4279):689–691.
- Burke V. J., Rathbun S. L., Bodie J. R., Gibbons J. W. 1998. Effect of density on predation rate for turtle nests in a complex landscape. *Oikos* 83:3–11.
- Caldwell J. P. 1986. Selection of egg deposition sites: a seasonal shift in the southern leopard frog, *Rana sphenoccephala*. *Copeia* 10(1):249–253.
- Carpenter C. C. 1966. Miscellaneous notes on Galapagos lava lizards (*Tropidurus-iguaniidae*). *Herpetologica* 26(3):377–386.
- Carpenter K. 1999. *Eggs, Nests, and Baby Dinosaurs: A Look at Dinosaur Reproduction*. Bloomington (IN): Indiana University Press.
- Carpenter K., Hirsch K. F., Horner J. R. 1994. *Dinosaur Eggs and Babies*. Cambridge (UK): Cambridge University Press.
- Carreno C. A., Harris R. N. 1998. Lack of nest defense behavior and attendance patterns in a joint nesting salamander, *Hemidactylium scutatum* (Caudata: Plethodontidae). *Copeia* 1998(1):183–189.
- Carter D. B. 1992. Reproductive ecology of the lace monitor *Varanus varius* in south-eastern Australia. Ph.D. thesis. Canberra (Australia): Australian National University.
- Christian K. A., Tracy C. R. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218–223.
- Congdon J. D., Gatten R. E., Jr. 1989. Movements and energetics of nesting *Chrysemys picta*. *Herpetologica* 45(1):94–100.
- Cooper W. E., Jr., Caffrey C., Vitt L. J. 1985. Aggregation in the banded gecko, *Coleonyx variegatus*. *Herpetologica* 41(3):342–350.
- Cooper W. E., Vitt L. J., Vangilder L. D., Gibbons J. W. 1983. Natural nest sites and brooding behavior of *Eumeces fasciatus*. *Herpetological Review* 14(3):65–66.
- Crump M. L. 1991. Choice of oviposition site and egg load assessment by a treefrog. *Herpetologica* 47:308–315.
- Crump M. L. 1995. Parental care. Pages 518–567 in *Amphibian Biology, Volume 2: Social Behaviour*, edited by H. Heatwole. Chipping Norton (Australia): Surrey, Beatty and Sons.
- Damman H., Cappuccino N. 1991. Two forms of egg defence in a chrysomelid beetle: egg clumping and excrement cover. *Ecological Entomology* 16(2):163–167.
- Danchin E., Wagner R. H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12(9):342–347.
- Danforth B. N. 1991. Female foraging and intranest behavior of a communal bee, *Perdita portalis* (Hymenoptera: Andrenidae). *Annals of the Entomological Society of America* 84(5):537–548.

- Deeming D. C., Ferguson M. W. J. 1991. *Egg Incubation: Its Effect on Embryonic Development in Birds and Reptiles*. London (UK): Cambridge University Press.
- Donnelly M. A., Guyer C. 1994. Estimating population size. Pages 183–200 in *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, edited by W. R. Heyer et al. Washington (DC): Smithsonian Institution Press.
- Doody J. S. 2006. Communal nesting in the red-throated skink, *Bassiana platynota*. *Herpetofauna* 36(1):23–24.
- Doody J. S., Sims R. A., Georges A. 2003b. Gregarious behavior of nesting turtles (*Carettochelys insculpta*) does not reduce predation risk. *Copeia* 2003(4): 894–898.
- Doody J. S., West P., Georges A. 2003a. Beach selection in pig-nosed turtles, *Carettochelys insculpta*. *Journal of Herpetology* 37(1):178–182.
- Doody J. S., Young J. E. 1995. Temporal variation in reproduction and clutch mortality of leopard frogs (*Rana utricularia*) in south Mississippi. *Journal of Herpetology* 29(4):614–616.
- Downie J. R., Disney R. H. L., Collins L., Hancock E. G. 1995. A new species of *Megaselia* (Diptera, Phoridae) whose larvae prey upon the eggs of *Leptodactylus fuscus* (Anura, Leptodactylidae). *Journal of Natural History* 29(4):993–1003.
- Downie J. R., Livingstone S. R., Cormack J. R. 2001. Selection of tadpole deposition sites by male trinidadian stream frogs, *Mannophryne trinitatis* (Dendrobatidae): an example of anti-predator behavior. *Herpetological Journal* 11(3):91–100.
- Drummond H. 1983. Adaptiveness of island nest-sites of green iguanas and slider turtles. *Copeia* 1983(2): 529–530.
- Duellman W. E., Trueb L. 1986. *Biology of Amphibians*. New York: MacGraw-Hill.
- Eckrich C. E., Owens D. W. 1995. Solitary vs. arribada nesting in the Olive Ridley sea turtles (*Lepidochelys olivacea*): a test of the predator-satiation hypothesis. *Herpetologica* 51(3):349–354.
- Emlen S. T. 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119(1):29–39.
- Espinoza R. E., Lobo F. 1996. Possible communal nesting in two species of *Liolaemus* lizards (Iguania: Tropiduridae) from northern Argentina. *Herpetological Natural History* 4(1):65–68.
- Fitch H. S. 1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. *University of Kansas Publications of the Museum of Natural History* 8:1–156.
- Forester D. C., Lykens D. V. 1988. The ability of wood frog eggs to withstand prolonged terrestrial stranding: an empirical study. *Canadian Journal of Zoology* 66:1733–1735.
- Foster W. A., Treherne J. E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293(5832):466–467.
- Freedberg S., Ewert M. A., Ridenhour B. J., Neiman M., Nelson C. E. 2005. Nesting fidelity and molecular evidence for natal homing in the freshwater turtle, *Graptemys kohnii*. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 272(1570):1345–1350.
- Galef B. G., Giraldeau L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour* 61(1):3–15.
- Giaretta A., Menin M. 2004. Reproduction, phenology and mortality sources of a species of *Physalasmus* (Anura: Leptodactylidae). *Journal of Natural History* 38(13):1711–1722.
- Giraldeau L.-A. 1997. The ecology of information use. Pages 42–68 in *Behavioral Ecology: An Evolutionary Approach*, Fourth Edition, edited by J. R. Krebs and N. B. Davies. Oxford (UK): Blackwell Scientific Publications.
- Giraldeau L.-A., Valone T. J., Templeton J. J. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 357(1427):1559–1566.
- Godfray H. C. J., Partridge J. L., Harvey P. H. 1991. Clutch size. *Annual Review of Ecology and Systematics* 22:409–429.
- Graves B. M., Duvall D. 1995. Aggregation in squamate reptiles associated with gestation, oviposition, and parturition. *Herpetological Monographs* 9:102–119.
- Greenberg B. 1943. Social behaviour of the western banded gecko, *Coleonyx variegates* Baird. *Physiological Zoology* 16:110–122.
- Greer A. E. 2004. Encyclopedia of Australian Reptiles. Australian Museum Online. <http://www.austmus.gov.au/herpetology/research/index.htm#encyclopedia> (accessed 15 February 2007).
- Guyétant R. 1966. Observations écologiques sur les pontes de *Rana temporaria* L. dans la région de Besançon. *Physiologie et Biologie Animale* 2:13–18.
- Håkansson P., Loman J. 2004. Communal spawning in the common frog *Rana temporaria*—egg temperature and predation consequences. *Ethology* 110:665–680.
- Hamilton W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7(1):1–52.
- Hamilton W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31(2):295–311.
- Harrison C. J. O. 1975. *A Field Guide to the Nests, Eggs and Nestlings of British and European Birds with North Africa and the Middle East*. London (UK): Collins.
- Harris R. N. 2008. Body condition and order of arrival

- affect cooperative nesting behaviour in four-toed salamanders *Hemidactylum scutatum*. *Animal Behaviour* 75(1):229–233.
- Harris R. N., Gill D. E. 1980. Communal nesting, brooding behavior, and embryonic survival of the four-toed salamander *Hemidactylum scutatum*. *Herpetologica* 36(2):141–144.
- Harris R. N., Hames W. W., Knight I. T., Carreno C. A., Vess T. J. 1995. An experimental analysis of joint nesting in the salamander *Hemidactylum scutatum* (Caudata: Plethodontidae): the effects of population density. *Animal Behaviour* 50(5):1309–1316.
- Hayes L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour* 59(4):677–688.
- Hayes M. P. 1983. Predation on the adults and pre-hatching stages of glass frogs (Centrolenidae). *Biotropica* 15:74–76.
- Hayes W. K., Carter R. L., Cyril S. Jr., Thornton B. 2004. Conservation of an endangered Bahamian rock iguana. I. Population assessments, habitat restoration, and behavioral ecology. Pages 232–257 in *Iguanas: Biology and Conservation*, edited by A. C. Alberts et al. Los Angeles (CA): University of California Press.
- Herreid C. F., Kinney S. 1967. Temperature and development of the wood frog *Rana sylvatica*, in Alaska. *Ecology* 48(4):579–590.
- Hess Z. J., Harris R. N. 2000. Eggs of *Hemidactylum scutatum* (Caudata: Plethodontidae) are unpalatable to insect predators. *Copeia* 2000(2):597–600.
- Hoffmann A., Resh V. H. 2003. Oviposition in three species of limnephiloid caddisflies (Trichoptera): hierarchical influences on site selection. *Freshwater Biology* 48(6):1064–1077.
- Horner J. R. 1982. Evidence of colonial nesting and 'site fidelity' among ornithiscian dinosaurs. *Nature* 297(5868):675–676.
- Horner J. R. 2000. Dinosaur reproduction and parenting. *Annual Review of Earth and Planetary Sciences* 28:19–45.
- Howard R. D. 1978. The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. *Ecology* 59(4):789–798.
- Howard R. D. 1980. Mating behaviour and mating success in woodfrogs, *Rana sylvatica*. *Animal Behaviour* 28(3):705–716.
- Huggins R. J., Thompson A. 1970. Communal spawning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. *Journal of Fish Biology* 2(1):53–54.
- Illano A. S., Fujinaga K., Nakao S. 2004. Mating, development and effects of female size on offspring number and size in the neogastropod *Buccinum isaotakii* (Kira, 1959). *Journal of Molluscan Studies* 70:277–282.
- Inman A. J., Krebs J. 1987. Predation and group living. *Trends in Ecology and Evolution* 2(2):31–32.
- Iverson J. B. 1990. Nesting and parental care in the mud turtle, *Kinosternon flavescens*. *Canadian Journal of Zoology* 68:230–233.
- Jockusch E. L., Mahoney M. J. 1997. Communal oviposition and lack of parental care in *Batrachoseps nigriiventris* (Caudata: Plethodontidae) with a discussion of the evolution of breeding behavior in plethodontid salamanders. *Copeia* 1997(4):697–705.
- Juterbock J. E. 1986. The nesting behavior of the dusky salamander, *Desmognathus fuscus*. I. Nesting phenology. *Herpetologica* 42:457–471.
- Karns D. R. 1992. Effects of acidic bog habitats on amphibian reproduction in a northern Minnesota peatland. *Journal of Herpetology* 26:401–412.
- Kearney M., Shine R., Comber S., Peardon D. 2001. Why do geckos group? An analysis of 'social' aggregations in two species of Australian lizards. *Herpetologica* 57(4):411–422.
- Kiesecker J. M., Blaustein A. R. 1997. Influences of egg laying behavior on pathogenic infection of amphibian eggs. *Conservation Biology* 11(1):214–220.
- Knapp C. R., Hudson R. D. 2004. Translocation strategies as a conservation tool for West Indian iguanas. Pages 199–209 in *Iguanas: Biology and Conservation*, edited by A. C. Alberts et al. Berkeley (CA): University of California Press.
- Koenig W. D., Stacey P. B. 1990. The acorn woodpecker: group living and food storage under contrasting ecological conditions. Pages 413–453 in *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*, edited by P. B. Stacey and W. D. Koenig. Cambridge (UK): Cambridge University Press.
- Koford R. R., Bowen B. S., Vehrencamp S. L. 1986. Habitat saturation in groove-billed anis (*Crotophaga sulcirostris*). *American Naturalist* 127(3):317–337.
- Koford R. R., Bowen B. S., Vehrencamp S. L. 1990. Groove-billed anis: joint nesting in a tropical cuckoo. Pages 335–355 in *Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior*, edited by P. B. Stacey and W. D. Koenig. Cambridge (UK): Cambridge University Press.
- Lalonde R. G., Mangel M. S. 1994. Seasonal effects on superparasitism by *Rhagoletis completa*. *Journal of Animal Ecology* 63(3):583–588.
- Laurila A., Seppä P. 1998. Multiple paternity in the common frog (*Rana temporaria*): genetic evidence from tadpole kin groups. *Biological Journal of the Linnean Society* 63(2):221–232.
- Layne J. N., Raymond M. A. V. 1994. Communal nesting of southern flying squirrels in Florida. *Journal of Mammalogy* 75(1):110–120.
- Loeb M. L. G., Bell L. K. 2006. Distribution of care-

- giving effort in a communally breeding lace bug: fair guarding without coercion. *Journal of Insect Behavior* 19(1):19–30.
- López-Ortiz R., Lewis A. R. 2002. Seasonal abundance of hatchlings and gravid females of *Sphaerodactylus nicholsi* in Cabo Rojo, Peurto Rico. *Journal of Herpetology* 36(2):276–280.
- Magnusson W. E., Lima A. P. 1984. Perennial communal nesting by *Kentropyx cacaratus*. *Journal of Herpetology* 18(1):73–75.
- Manning C. J., Dewsbury D. A., Wakeland E. K., Potts W. K. 1995. Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour* 50(3):741–751.
- Marco A., Díaz-Paniagua C., Hidalgo-Vila J. 2004. Influence of egg aggregation and soil moisture on incubation of flexible-shelled lacertid lizard eggs. *Canadian Journal of Zoology* 82(1):60–65.
- Márquez R., Verrell P. 1991. The courtship and mating of the Iberian midwife toad, *Alytes cisternasii* (Amphibia: Anura: Discoglossidae). *Journal of Zoology* 225:125–139.
- Martens A., Rehfeldt G. 1989. Female aggregation in *Platycypha caligata* (Odonata: Chlorocyphidae): a tactic to evade male interference during oviposition. *Animal Behaviour* 38(3):369–374.
- Maynard Smith J. 1982. *Evolution and the Theory of Games*. Cambridge (UK): Cambridge University Press.
- McDiarmid R. W., Gorzula S. 1989. Aspects of the reproductive ecology and behavior of the Tepui toads, genus *Oreophrynella* (Anura, Bufonidae). *Copeia* 1989(2):445–451.
- McGowan K. J., Woolfenden G. E. 1989. A sentinel system in the Florida scrub jay. *Animal Behaviour* 37(6):1000–1006.
- McMillan V. E. 2000. Aggregating behavior during oviposition in the dragonfly *Sympetrum vicinum* (Hagen) (Odonata: Libellulidae). *American Midland Naturalist* 144(1):11–18.
- Messina F. J. 1998. Maternal influences on larval competition in insects. Pages 227–243 in *Maternal Effects as Adaptations*, edited by T. A. Mousseau and C. W. Fox. Oxford (UK): Oxford University Press.
- Meylan A. B., Bowen B. W., Avise J. C. 1990. A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science* 248(4956):724–727.
- Michener C. D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Cambridge (MA): Belknap Press of Harvard University Press.
- Mora J. M. 1989. Eco-behavioral aspects of two communally-nesting iguanines and the structure of their shared burrows. *Herpetologica* 45:293–298.
- Myers J., Loveless M. D. 1976. Nesting aggregations of the euglossine bee *Euplusia surinamensis* (Hymenoptera: Apidae): individual interactions and the advantage of living together. *Canadian Entomologist* 108:1–6.
- Noble G. K., Mason E. R. 1933. Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *American Museum Novitates* 619:1–29.
- Nussbaum R. A. 2003. Parental care. Pages 527–612 in *Reproductive Biology and Phylogeny, Volume 1: Urodela*, edited by D. Sever. Enfield (NH): Science Publishers.
- OVaska K., Caldbeck J., Lazell J. 1998. *Eleutherodactylus schwartzi* (NCN) Reproduction. *Herpetological Review* 29(2):97.
- Papaj D. R., Averill A. L., Prokopy R. J., Wong T. T. Y. 1992. Host-marking pheromone and use of previously established oviposition sites by the Mediterranean fruit fly (Diptera: Tephritidae). *Journal of Insect Behavior* 5(5):583–598.
- Paton P. W. C., Egan R. S., Osenkowski J. E., Raithe C. J., Brooks R. T. 2003. *Rana sylvatica* breeding behavior during drought. *Herpetological Review* 34: 236–237.
- Peckarsky B. L., Taylor B. W., Caudill C. C. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia* 125(2):186–200.
- Perry G., Dmi'el R. 1994. Needles and haystacks: searching for lizard eggs in a coastal sand dune. *Amphibia-Reptilia* 15:395–401.
- Petranka J. W., Fakhoury K. A. 1991. Evidence of a chemically-mediated avoidance response of ovipositing insects to bluegills and green frog tadpoles. *Copeia* 1991:234–239.
- Pilastro A. 1992. Communal nesting between breeding females in a free-living population of fat dormouse (*Glis glis* L.). *Bolletín Zoologia* 59:63–68.
- Platnick N. I. 1991. Patterns of biodiversity: tropical vs. temperate. *Journal of Natural History* 25:1083–1088.
- Pleguezuelos J. M., Galán P., Fernández-Cardenete J. R. 2004. Communal nesting of *Psammotromus algirus* (Linnaeus, 1758), under extreme environmental conditions. *Amphibia-Reptilia* 25:333–336.
- Plummer M. V. 1981. Communal nesting of *Opheodrys aestivus* in the laboratory. *Copeia* 1981:243–246.
- Pough F. H., Andrews R. M., Cadle J. E., Crump M. L., Savitzky A. H., Wells K. D. 2004. *Herpetology*. Third Edition. Upper Saddle River (NJ): Benjamin Cummings/Pearson Education.
- Pruett-Jones S. 1992. Independent versus nonindependent mate choice: do females copy each other? *American Naturalist* 140(6):1000–1009.
- Radder R. S., Shine R. 2007. Why do female lizards lay their eggs in communal nests? *Journal of Animal Ecology* 76(5):881–887.
- Rand A. S. 1967. Communal egg laying in anoline lizards. *Herpetologica* 23:227–230.

- Rand A. S. 1968. A nesting aggregation of iguanas. *Copeia* 1968(3):552–561.
- Rand A. S., Dugan B. 1983. Structure of complex iguana nests. *Copeia* 1983(3):705–711.
- Rand W. M., Rand A. S. 1976. Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. *Zeitschrift für Tierpsychologie* 40:279–299.
- Rand A. S., Rand W. M. 1978. Display and dispute settlement in nesting iguanas. Pages 245–251 in *Behavior and Neurology of Lizards: An Interdisciplinary Colloquium*, edited by N. Greenberg and P. D. MacLean. Rockville (MD): National Institute of Mental Health.
- Rauch N. 1988. Competition of marine iguana females (*Amblyrhynchus cristatus*) for egg-laying sites. *Behaviour* 107(1–2):91–106.
- Reading C. J., Clarke R. T. 1988. Multiple clutches, egg mortality and mate choice in the mid-wife toad, *Alytes obstetricans*. *Amphibia-Reptilia* 9:357–364.
- Resetarits W. J., Jr. 1996. Oviposition site choice and life history evolution. *American Zoologist* 36(2):205–215.
- Resetarits W. J., Jr., Wilbur H. M. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70:220–228.
- Reynolds J. D., Goodwin N. B., Freckleton R. B. 2002. Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 357(1419):269–281.
- Roberts W. E. 1994. Explosive breeding, aggregations and parachuting in a neotropical frog, *Agalychnis saltator* (Hylidae). *Journal of Herpetology* 28(2):193–199.
- Robinson C., Bider J. R. 1988. Nesting synchrony: a strategy to decrease predation of snapping turtle, *Chelydra serpentina*, nests. *Journal of Herpetology* 22:470–473.
- Rosenzweig M. L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137(supplement: habitat selection):S5–S28.
- Rudolf V. H. W., Rödel M.-O. 2005. Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. *Oecologia* 142(2):316–325.
- Ryan M. J. 1985. *The Túngara Frog: A Study in Sexual Selection and Communication*. Chicago (IL): University of Chicago Press.
- Schulte J. A., II, Valladares J. P., Larson A. 2003. Phylogenetic relationships within Iguanidae using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica* 59:399–419.
- Seale D. B. 1982. Physical factors influencing oviposition by the wood frog, *Rana sylvatica*, in Pennsylvania. *Copeia* 1982:627–635.
- Sexton O. J. 1975. Black vultures feeding on iguana eggs in Panama. *American Midland Naturalist* 93(2):463–468.
- Seymour R. S. 1995. Oxygen uptake by embryos in gelatinous egg masses of *Rana sylvatica*: the roles of diffusion and convection. *Copeia* 1995:626–635.
- Shine R. 1979. Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetologica* 35:1–11.
- Shine R. 1988. Parental care in reptiles. Pages 275–329 in *Biology of the Reptilia, Ecology B: Defense and Life History, Volume 16*, edited by C. Gans and R. B. Huey. New York: Alan R. Liss Inc.
- Shine R. 1991. Strangers in a strange land: ecology of the Australian colubrid snakes. *Copeia* 1991(1):120–131.
- Smith G., Trumbo S. T., Sikes D. S., Scott M. P., Smith R. L. 2007. Host shift by the burying beetle, *Nicrophorus pustulatus*, a parasitoid of snake eggs. *Journal of Evolutionary Biology* 20(6):2389–2399.
- Spencer R. J. 2002. Experimentally testing nest site selection: fitness tradeoffs and predation risk in turtles. *Ecology* 83(8):2136–2144.
- Stamps J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131(3):329–347.
- Stamps N. E. 1980. Egg deposition patterns in butterflies: Why do some species cluster their eggs rather than deposit them singly? *American Naturalist* 115(3):367–380.
- Strathmann R. R., Strathmann M. E. 1995. Oxygen supply and limits on aggregation of embryos. *Journal of the Marine Biology Association of the United Kingdom* 75:413–428.
- Sutherland W. J. 1996. *From Individual Behavior to Population Ecology*. New York: Oxford University Press.
- Sweeney B. W., Vannote R. L. 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* 36:810–821.
- Tallamy D. W. 1985. 'Egg dumping' in lace bugs (*Gargaphia solani*, Hemiptera: Tingidae). *Behavioral Ecology and Sociobiology* 17(4):357–362.
- Tallamy D. W. 2005. Egg dumping in insects. *Annual Review of Entomology* 50:347–370.
- Test F. H., Heatwole H. 1962. Nesting sites of the red-backed salamander, *Plethodon cinereus*, in Michigan. *Copeia* 1962:206–207.
- Tinkle D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 132:1–182.
- Townsend T. M., Larson A., Louis E., Macey J. R. 2004. Molecular phylogenetics of Squamata: the position of snakes, Amphisbaenians and Dibam-

- ids, and the root of the Squamate tree. *Systematic Biology* 53(5):735–757.
- Treisman M. 1975. Predation and the evolution of gregariousness: I. Models for concealment and evasion. *Animal Behaviour* 23(4):779–800.
- Trivers R. L. 1974. Parent-offspring conflict. *American Zoologist* 14(1):249–264.
- Turner G. F., Pitcher T. J. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist* 128(2):228–240
- Vehrencamp S. L. 1978. The adaptive significance of communal nesting in groove-billed anis (*Crotophaga sulcirostris*). *Behavioral Ecology and Sociobiology* 4(1):1–33.
- Vieites D. R., Nieto-Roman S., Barluenga M., Palanca A., Vincas M., Meyer A. 2004. Post-mating clutch piracy in an amphibian. *Nature* 431(7006):305–308.
- Villa J., McDiarmid R. W., Gallardo J. M. 1982. Arthropod predators of leptodactylid frog foam nests. *Brenesia* 19–20:577–589.
- Vitt L. J. 1993. Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. *Canadian Journal of Zoology* 71:2370–2390.
- Vitt L. J., Zani P. A., Monteiro De Barros A. A. 1997. Ecological variation among populations of the gekkonid lizard *Gonatodes humeralis* in the Amazon basin. *Copeia* 1997(1):32–43.
- Waldman B. 1982. Adaptive significance of communal oviposition in wood frogs (*Rana sylvatica*). *Behavioral Ecology and Sociobiology* 10(3):169–174.
- Waldman B., Ryan M. J. 1983. Thermal advantages of communal egg mass deposition in wood frogs (*Rana sylvatica*). *Journal of Herpetology* 17:70–72.
- Ward S. A., Kukuk P. F. 1998. Context-dependent behaviour and the benefits of communal nesting. *American Naturalist* 152(2):249–263.
- Warkentin K. M. 2000. Wasp predation and wasp-induced hatching of red-eyed treefrog eggs. *Animal Behaviour* 60(4):503–510.
- Wells K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25(3):666–693.
- Werner D. I. 1983. Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galapagos: clutch size and migration costs. *American Naturalist* 121(6):757–775.
- Werner Y. L. 1986. Ecology of eggs and laying sites of *Ptyodactylus* geckos. Pages 441–444 in *Studies in Herpetology: Proceedings of the European Herpetological Meeting*, edited by Z. Roček. Prague (Czech Republic): Charles University Press.
- Wiewandt T. A. 1982. Evolution of nesting patterns in iguanine lizards. Pages 119–141 in *Iguanas of the World: Their Behavior, Ecology, and Conservation*, edited by G. M. Burghardt and A. S. Rand. Park Ridge (NJ): Noyes Publications.
- Wilson E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge (MA): Belknap Press of Harvard University Press.
- Wrona F. J., Dixon R. W. J. 1991. Group size and predation risk: a field analysis of encounter and dilution effects. *American Naturalist* 137(2):186–201.
- Zina J. 2006. Communal nests in *Physalaemus pustulosus* (Amphibia: Leptodactylidae): experimental evidence for female oviposition preferences and protection against desiccation. *Amphibia-Reptilia* 27(1):148–150.
- Zink A. G. 2000. The evolution of intraspecific brood parasitism in birds and insects. *American Naturalist* 155(3):395–405.
- Zink A. G. 2001. The optimal degree of parental care asymmetry among communal breeders. *Animal Behaviour* 61(2):439–446.
- Zink A. G. 2005. The dynamics of brood desertion among communally breeding females in the treehopper, *Publilia concava*. *Behavioral Ecology and Sociobiology* 58(5):466–473.
- Zwick H., Zwick P. 1990. Terrestrial mass-oviposition of *Prosimulium* species (Diptera: Simuliidae). *Aquatic Insects* 12(1):33–46.
- Zug G. R., Vitt L. J., Caldwell J. P. 1991. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. San Diego (CA): Academic Press.