Forum: Invited Review

Parental-care parasitism: how do unrelated offspring attain acceptance by foster parents?

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In this review, we describe a new term, "parental-care parasitism", that we define as the interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating its own costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts). Parental-care parasitism comprises parasitic behaviors ranging from interactions in which just the nest is taken over to those where various combinations of nest, food and offspring care are parasitized. We subdivide parental-care parasitism into 3 categories depending on the strategy used by the parasite to reach host nest: 1) the parasite approaches the nest during host absence, 2) parasite and host adults meet at the nest but no aggression is carried out, or 3) the host tries to evict the parasite at the nest. We also discuss the costs and benefits for both parents and offspring, as well as for hosts and parasites, placing different forms of parental-care parasitism in an evolutionary context within the frameworks of both parental investment theory and coevolutionary arms race theory. Herein, we thoroughly discuss the lack of offspring discrimination found in some species, some populations of the same species and some individuals within the same population on the basis of the coevolutionary arms race theory, and the fact that unrelated offspring attain acceptance by foster parents, contrary to the general predictions of parental investment theory. This review offers a conceptual framework that seeks to link parental investment theory with coevolutionary arms race theory. *Key words:* brood parasitism, coevolution, parasitism, parental care, parental-care parasitism, parental investment. *[Behav Ecol 22:679–691 (2011)]*

INTRODUCTION

Parental care involves any sort of parental behavior that increases the fitness of assisted offspring (Clutton-Brock 1991). Parental care has been described in most animal phyla but is especially well developed in numerous species of insects, crustaceans, and vertebrates (Glazier 2002). The amount of parental care provided to offspring by different species is determined mainly by ecological factors that increase mortality of eggs or young, such as harsh physical conditions, difficulty of access to resources, and a high risk of predation of eggs or young (Clutton-Brock 1991; Glazier 2002).

Parental care is a highly variable behavioral trait between species. It ranges from nest construction to a combination of nest preparation, feeding, cleaning, and defense of the offspring. Many different behavioral traits have evolved within the animal kingdom that help offspring to survive the initial stages of life, with the parents providing nutrients, warmth, protection from enemies, and the elements, a favorable nest environment and/or opportunities for learning the skills needed for survival or reproduction (Glazier 2002). Parental investment theory suggests that such variation arises from interspecific differences in the trade-offs between the fitness benefits for offspring and the fitness costs to parents (Clutton-Brock 1991).

In many species, parental care is one of the most energy-consuming activities that affect an individual's fitness (Trivers 1972; Clutton-Brock 1991). Parental investment involves important costs, such as a greater predation risk and large expenditure of time and energy (Clutton-Brock and Vincent 1991; Smith and Wootton 1995). Parental investment theory assumes that parental care is the evolutionary product of fitness costs and benefits; thus parents should be able to increase their fitness by trading off present and future parental investment (Trivers 1972; Carlisle 1982; Winkler 1987; Montgomerie and Weatherhead 1988; Clutton-Brock and Vincent 1991). In agreement with this, it is well known that parents are able to favor offspring of higher reproductive value (Lyon et al. 1994; Rytkönen 2002; Bize et al. 2006; Smiseth et al. 2007; Griggio et al. 2009).

Because parental care is costly and it is important for parents to save energy for subsequent reproductive events, parental investment theory predicts that parents should not provide assistance to young animals that are not their own genetic offspring. That is, parents should reduce or avoid care for unrelated offspring to save energy or other resources for future reproductive events. This is usually the case with paternal care in response to a reduced certainty of paternity not only in birds (Westneat and Sherman 1993; Sheldon et al. 1997; Møller and Cuervo 2000) but also in fish (Neff 2003a) and arthropods (Zeh and Smith 1985).

However, the capacity to recognize and discriminate against unrelated offspring has been shown to be well developed in some species (Buckley PA and Buckley FG 1972; Balcombe 1990; Phillips and Tang-Martinez 1998; Insley 2000; Searby and Jouventin 2003; Searby et al. 2004; Jesseau et al. 2008; Li and Zhang 2010) but not in others (Davies and Brooke 1989; Rothstein 1990; Moksnes et al. 1991; Davies 2000). Because parental care is beneficial only if directed toward genetic descendants (Trivers 1972), why then do parents sometimes care for unrelated offspring that parasitize

parental care? This essential question is addressed in the GENERAL DISCUSSION.

The term "parasitism" includes those interactions in which one or several individuals (parasites) obtain benefits from other individuals (hosts), thereby decreasing the hosts' fitness. Thus, parasitism always affects host fitness and so host species are usually under strong selection pressures to develop defensive strategies (defenses) against their parasites, which may cause the parasites to improve their parasitic strategies (counterdefenses). This process is known as an "arms race" (Dawkins and Krebs 1979) and it usually occurs within a coevolutionary process that implies reciprocal evolutionary change in both the parasite and the host species (Thompson 1994)—but not always (see Janzen 1980).

We define "parental-care parasitism" as an interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating the costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts). Thus, cases that include the parasitism of a resource prepared for direct use by the offspring are also encompassed within this term. Parental-care parasitism exists both at intraspecific and interspecific levels. This distinction is sometimes important because the costs to hosts and the virulence of parasites in each case are clearly under different constraints and selective pressures.

Within the term "parental-care parasitism," we include such behaviors as nest usurpation and theft of stored food, leaving parasitic offspring to be defended and fed by other individuals, and exploitation of worker labor in eusocial animals. We also include those cases in which it is the offspring itself who seek parasitism. Most cases of parental-care parasitism have been previously labeled "brood parasitism", but in some cases, they have been referred to as "reproductive parasitism," "kleptoparasitism," "kleptobiosis," and "social parasitism"; basing the classification mainly on the type of resource parasitized. This imprecise terminology is problematic to the study of host-parasite relationships because there is confusion over what each particular term means and how each should be used. This problem with terminology, and the fact that the costs incurred by hosts are highly different across different host-parasite systems, as we will describe below, are the reasons why we propose a new classification, based on behavior of both parasite and host, which will be useful when comparing different parasitic interactions involving parental care. The main objective of this review is to present a new classification of parental-care parasitism in an evolutionary context within the frameworks of both parental investment theory and coevolutionary arms race theory.

We resolve the terminological issues by discussing cases of parasitic interactions that involve parental care, and the different adaptations that they present, along a parasitic behavioral gradient that we have divided into 3 categories: 1) the parasite approaches the nest during host absence, 2) parasite and host adults meet at the nest but no aggression is carried out, and 3) the host tries to evict the parasite at the nest (Table 1). In addition to the behavior of the parasite, we further subdivided according to defensive mechanisms evolved by the host against its enemies and the possible coevolutionary arms race that has driven the process. Our selection of examples is biased in favor of those that outline a general rule or those in which individuals incur higher than expected costs. The review is also biased toward insect taxa, which is unsurprising given that 95% of all described species are arthropods (Hawksworth and Kalin-Arroyo 1995). This review offers a conceptual framework that seeks to link parental investment theory with coevolutionary arms race theory.

PARENTAL-CARE PARASITISM AND BEHAVIORAL CLASSIFICATION

We classify parental-care parasitism depending on the parasite strategy that used to approach the nest, mainly whether the parasitic female avoids the host or not to perform parasitism. Then, we subdivided each section depending on whether the host has developed defenses to the parasitism or not (see Table 1). We discuss each example under both parental-care investment and coevolutionary arms race theories whenever possible.

Table 1

Behavioral classification of parental-care parasitism

Parasite performance	Host behavioral response		Taxon
Parasitism during host absence	Without defense or counter-adaptation		Hymenoptera Anura
	Defense	Adults could meet	Hymenoptera[a] Araneae
		Adults never meet	Hymenoptera
Parasite and host meet without aggression	Without defense or counter-adaptation		Heteroptera
			Lepidoptera
			Siluriformes
	With defense		Hymenoptera[a]
			Coleoptera
	Possible aggression between host and parasite		Perciformes
			Rodentia[a]
	With counteradaptation		Hymenoptera
Parasite and host meet with aggression	Without offspring recognition		Apodiformes
			Falconiformes
			Stigiformes
			Hymenoptera[a]
	With offspring recognition		Coleoptera[a]
			Aves[a,b]

Classification of parental-care parasitism based on parasite behavior while approaching the host nest and on the host response to parasite attack. Also included are the taxa corresponding to each interaction.

[a] Host recognition of parasite offspring.

[b] Avian orders included are: Anseriformes, Charadriformes, Ciconiformes, Cuculiformes, Falconiformes, Galliformes, Passeriformes, Piciformes, Spheniciformes, and Stigiformes.

Parasitism performed during host absence

In some occasions, parasites approach host nest to perform parasitism when host is away, either because the host is not at the nest when the parasite arrives or because the parasite wait until the host leaves. In these 2 situations, host can both present defenses or do not, surely depending on the cost that this parasitism means to it and the duration of coevolutionary relationships between the parasite and the host species.

Without defense or counteradaptation

In many species, as in most non-eusocial Hymenoptera, parental care consists on providing a proper place and food to ensure an optimal development of the offspring. Thus, parents will leave the nest while foraging and/or permanently after oviposition. In these species, parasitism is usually performed while the host is away foraging as happens in some Megachilid bees and Eumenid and Ammophiline (Family: Sphecidae) wasps (Field 1992a). The parasite enters a conspecific's nest, discard host eggs or small larvae (when present), and lay its own eggs after provision the cell. If the cell was already partially provisioned, the parasite's offspring will also eat this food. After parasitism, the female closes the nest entrance. In these occasions, host and parasitic females never met and had not been described any defense against parasitism, even when the parasitic pressure could reach high percentages (36% in the case of the eumenid wasp *Zethus miniatus*) (Field 1992a). In other Megachilids, as in *Cerceris intricata* or *Crabro monticola*, when parasitism has been performed, host adopts the parasitic strategy itself (Field 1992a).

Also, an unusual example has been reported recently in *Dendrobates variabilis*, an Amazonian poison frog. Adult males carry and deposit their tadpoles within pools containing the eggs of unrelated conspecifics, which serve as food for cannibalistic tadpoles (Brown et al. 2008). Although this parasitic interaction mainly occurs at an intraspecific level, interspecific interactions have also been described (*D. variabilis* adpoles also kill and consume *D. imitator* ones; Brown et al. 2008).

With defense

In accordance to parental investment theory, parents should defend their nest and offspring (Clutton-Brock 1991). These defenses could be either active or passive. The most intuitive and common defense against parasites is to fight them off the nest, but in the examples discussed in this section, the parasitism is performed while host is away, so the host can mainly develop passive defenses.

Adults could meet

Even if the parasitism is performed while host is away, both host and parasite could meet at the nest. In these cases, the most common defense is to try to drive off the parasite. Field (1992a) reviewed intraspecific parasitism in nest-building wasps and bees. In some parasitic interactions, as in ground-nesting Sphecid wasps and 2 Megachilid bees (*Haplitis anthocopoides* and *Chalicodoma pyrenaica*), the author describes that if both host and parasitic females meet at the nest they fight for it.

Furthermore, all species within the genus *Sapyga* (Hymenoptera: Sapygidae) are known to be obligate interspecific nest parasites of solitary bees, in particular of the megachilid genera *Osmia*, *Megachile*, and *Chelostoma* (Münster-Swendsen and Calabuig 2000). *Sapyga* parasitic female wasps enter host nests to oviposit while the owner is away. When parasitism is successful, first instar parasitic larvae kill and consume the egg or larvae of the host as well as the nectar and pollen provisions in the cell (Torchio 1972), thereby reducing host fitness.

Both passive and active defensive traits have been described for this interaction. As a passive defense, host females spend more time at the nest entrance (e.g., in *Osmia pumila*) or nest communally (Goodell 2003). Also, when interspecific parasites are common, some solitary bee species oviposit within several nests (e.g., in *O. pumila*), increasing the odds that at least some nests will escape parasitism (Goodell 2003). On the other hand, it is surprising that solitary bees rarely attack parasites approaching nests (Wcislo and Cane 1996). But if hosts and parasites meet at the nest, the host female can actively defend her nest and aggressively evicts the parasite (*Megachile rotundata*; Torchio 1972; Goodell 2003). Moreover, as happens in many avian host species of brood parasites (Davies 2000), a very effective host defense is the recognition and subsequent destruction of parasitic eggs (e.g., in *Chelostoma florisomne*, Münster-Swendsen and Calabuig 2000) where host females vigorously clean the nest removing parasitic eggs and even some stored pollen (Münster-Swendsen and Calabuig 2000). The female megachilid is apparently efficient in detecting parasite eggs. However, egg recognition has not been described in other bee species. Perhaps, weaker selection pressures due to a lower cost of parasitism, or the existence of other defensive mechanisms that protect the host from the parasite, account for the rarity with which egg-recognition behavior arises (see GENERAL DISCUSSION). In any case, females of some parasitic species (e.g., *Sapyga clavicornis*) are capable of penetrating a recently finished cell cap with the pointed tip of the abdomen, after which they oviposit inside the cell (Münster-Swendsen and Calabuig 2000). The most surprising antiparasite defense may involve the construction of an empty cell in front of brood cells. Thus, a parasite will oviposit in an unprovisioned brood cell and its offspring will die of starvation (*C. florisomne*; Münster-Swendsen and Calabuig 2000). This defensive strategy decreases the rate of parasitism from 28.9% to 5.4% (Münster-Swendsen and Calabuig 2000). The evolution of empty cell construction appears to be the direct consequence of selective pressures imposed by the brood parasites of *C. florisomne* because, as Parker (1988) has pointed out, in 2 other *Chelostoma* species populations without nest parasites, the females do not build empty cells.

On the other hand, Boulton and Polis (2002) describe the only example of which we are aware of nest parasitism within the order Araneae. The spider *Diguetia mojavea* (Araneae: Diguetidae) is parasitized mainly (76%) by 2 salticid species (*Metaphidippus manni* and *Habronattus tranquillus*) whose spiderlings also prey on those of the host (Boulton and Polis 2002). Possible host defense have been reported for *D. mojavea*. Only 0.6% of the host nests were parasitized in the presence of the host mother but the rate jumped to 81% when the mother was absent. Although it is not described how this defensive mechanism is developed, we could assume that it is an active defense. Furthermore, the large number of eggs laid by the host (1000 against only a few parasite eggs) has also been interpreted as a passive defensive mechanism because a larger clutch increases the probability that some host offspring will survive (Jackson 1978; Boulton and Polis 1999).

Adults never meet

Sometimes host female returns to her nest from foraging and find it parasitized. In these occasions, some species do not present defenses (as discussed above), but some others have developed defensive behaviors. These interactions have been thoroughly studied in ground-nesting crabronid wasps (subfamilies Larrinae, Crabroninae, Nyssoninae, and Philanthinae). In his review of the phenomenon, Field (1992a) described how the usurper usually secures the host's nest before provisioning it. Nest usurpation often occurs while the original occupant is away hunting for prey. When the parasite closes the nest, the

returning host can dig through the closure and attempt to evict the parasite (e.g., in *Lindenius columbianus, C. monticola*).

Sometimes, both host and parasite never meet but host presents behavioral defenses against parasitism even if it would be performed when the host is absent. In these cases, we can expect that parasitic rate should be high or parasitism costly enough to drive the host to develop defensive strategies. A good example of these interactions is the case of superparasitism in hymenopteran parasitoids. In the parasitoids' breeding strategy, the main parental cost is to find a suitable prey to lay the eggs. In cases of superparasitism, a parasitoid female deposits her egg(s) on a prey item that has already been victimized by other female, avoiding the main cost of breeding (see the review by Dorn and Beckage (2007) for more details). As Field (1992b) stated, superparasitism in ectoparasitoids competing sequentially for the same host is functionally equivalent to brood parasitism. In this context, conspecific superparasitism can be interpreted as a kind of parental-care parasitism, in which the second comer parasitizes parental efforts by the first one. In any event, the original parasitoid loses if the second comer can destroy the eggs of the former by stabbing them with her ovipositor within the host before laying her own eggs (e.g., in *Encarsia formosa*; Hymenoptera: Aphelinidae; Dorn and Beckage 2007) or if there is competition for food between the 2 groups of larvae. Thus, as commented above, being parasitized represents an extra cost to the host, whose reproductive effort will be reduced to zero.

The costs to the host of this type of parasitism are high and so it would be expected to develop some counteradaptations. Dorn and Beckage (2007) describe some defensive adaptations against superparasitism. For example, the original female may lay many eggs on the prey (e.g., *Trichogramma evanesens*; Hymenoptera: Trichogrammatidae), making it inappropriate for subsequent females. Another defense under conditions of massive superparasitism is a reduction in clutch size, which could prevent host death and increase the odds of survival for a latecomer (e.g., *Cotesia sp.*; Hymenoptera: Braconidae; Dorn and Beckage 2007). The latter could be seen as a case of tolerance instead of resistance (see GENERAL DISCUSSION).

Parasite and host meet without aggression

Sometimes parasite and host meet but do not fight even if parasitism is performed when host female is present. In other occasions it is the offspring itself that perform parasitism and the host is completely cheated (see *Maculinea* larvae example below).

Without defense or counter-adaptation

The most intriguing example has been described in golden egg bugs *Phyllomorpha laciniata* (Hemiptera: Coreidae) where individuals are parasitized without showing any resistance even when it rises the odds of being predated (Kaitala 1996; Kaitala 1998; García-González and Gomendio 2003).

Golden egg bugs *Phyllomorpha laciniata* (Hemiptera: Coreidae) carry their eggs on their backs, which is advantageous because eggs laid on vegetation suffer very high mortality (97%; García-González and Gomendio 2003). Golden egg bug females glue eggs on the backs of other individuals of both sexes (Kaitala 1996). Egg carrying behavior is a costly form of parental care because individuals with eggs on its backs become more conspicuous and are more frequently attacked by predators than are egg-free ones (Kaitala 1996; Kaitala 1998; García-González and Gomendio 2003). Some eggs are laid on the back of the male that fertilized them and, in this case, egg-carrying behavior can be considered potentially adaptive parental care. However, according to Tay et al. (2003), 87% of the eggs carried by a mated

male have been fertilized by another male or males. In this case, the hypothesis of parasitic behavior may apply.

It is surprising that individuals do not resist attempts by females to lay eggs on them (Kaitala 1996). Moreover, although egg-caring males are able to remove some of the eggs glued on their backs, they cannot distinguish their offspring from the rest (Kaitala 1998), which implies high costs for egg carriers if they remove their own eggs.

Another intriguing parasitic interaction in which no defensive mechanisms have been developed is described in one of the most advanced parental care behaviors known among fish, in mouthbrooding cichlids (Sato 1986). Eggs of the mouthbrooder are usually picked up by the female immediately after oviposition and are incubated in her buccal cavity. After yolk sac absorption, the fry frequently swim out to forage and return, using the mouth as a refuge until they become fully independent (Sato 1986). Sato (1986) found that a Lake Tanganyika endemic mochokid catfish species, *Synodontis multipunctatus*, is an interspecific parental-care parasite of at least 6 species of mouthbrooding cichlids. Presumably, the female catfish lays her eggs at the same time as her host, which picks them up together with her own eggs. Once inside the host female's buccal cavity, they develop together with host fry (Sato 1986). But catfish parasitic offspring hatch earlier than those of the host and feed on them (Sato 1986), which, as commented above, implies an extra cost of parasitism to the host dramatically reducing its reproductive effort.

No counterparasitic defense mechanisms have been described in mouthbrooding cichlid fish. Perhaps the low parasitic pressure (the parasitism rate in different species ranges between 1.4% and 15%; mean = 6.3%; Sato 1986) is not strong enough for a counteradaptive strategy to evolve or, more probably, expelling catfish eggs incurs greater losses than benefits, as happens in some hosts of avian brood parasites (Davies 2000) as we discuss below.

Also offspring can seek parasitism without aggressive host responses. The larvae of several species of *Maculinea* butterflies (Lepidoptera: Lycaenidae) seek to parasitize the parental care of a certain nests of *Myrmica* ants (Formicidae). Butterfly females lay their eggs on host plants where their brood successfully grows by feeding on flowers. Subsequently, the fourth instar larvae descend to the ground where they attract ant workers by producing a cocktail of hydrocarbons that mimic the larvae of *Myrmica* ants (Akaino et al. 1999). Workers carry caterpillars inside the nest, where the latter use a combination of tactile, acoustic and behavioral signals to get the ants to adopt them (Akaino et al. 1999). Inside the nest, caterpillars either get the worker ants to feed them (Elmes et al. 1991a, 1991b) or themselves prey on the ant brood (Thomas and Wardlaw 1992). As a result, *Maculinea* larvae gain about 98% of their final weight in the ant nest during the 11 or 23 months (depending on species) that they spend within it (Steiner et al. 2003). This parasitism harms the ant host by monopolizing worker care and/or by inflicting losses on the ant brood. It is surprising that no defenses against this parasitism have been reported.

On the other hand, one of the most advanced parental care behaviors known among fish is described in mouthbrooding cichlids (Keenleyside 1979, in Sato 1986). Eggs of the mouthbrooder are usually picked up by the female immediately after oviposition and are incubated in her buccal cavity. After yolk sac absorption, the fry frequently swim out to forage and return, using the mouth as a refuge until they become fully independent (Baerends and Baerends-Van-Roon 1950; Fryer and Iles 1972; in Sato 1986). Sato (1986) found that a Lake Tanganyika endemic mochokid catfish species, *Synodontis multipunctatus*, is an interspecific parental-care parasite of at least 6 species of mouthbrooding cichlids. Presumably, the female

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With behavioral defense
In some occasions, both host and parasite meet but hosts do not try to drive off the parasite; on the contrary, they present passive defense against parasitism. A clear example is the interspecific parasitism that takes place in *Parastizopus armaticeps* (Coleoptera: Tenebrionidae). Both host parents collaborate in digging a burrow, guarding the nest and collecting plant detritus to feed their offspring (Rasa 1999). Parasitic females of the tenebrionid *Eremostibes opacus* enter nests of *P. armaticeps*, where they feed, oviposit and then leave (Rasa 1996). The parasitic larvae live in the sand under the detritus store and feed on it (Rasa 1996), reducing the food resources for both host parents and offspring (Geiselhardt et al. 2006). Studies by Rasa and Heg (2004) showed that 90% of *P. armaticeps* burrows are parasitized. Parasitic females avoid being attacked by host parents because of their chemical mimicry (Rasa and Heg 2004). When researchers experimentally introduced parasites in host nests, only 7% of host individuals ejected the parental parasites, after detecting them via olfactory cues. Other potential defensive behaviors against parasitic females have been described, such as when *P. armaticeps* parents (mainly males) guard the burrow entrance. This defensive strategy, although probably evolved to evict same-sex intruders, could also repel nest parasites (Rasa 1999).

Another typical parasitic interaction where no aggression against the parasite occurs has been reported in eusocial Hymenoptera (ants, wasps, and bees) that are vulnerable to parasitic laying by individual workers (Oldroyd 2002). This parasitic interaction has been thoroughly reviewed for eusocial bees by Beekman and Oldroyd (2008). They discuss different kinds of worker parasitism: intracolony intraspecific parasitism in queenright colonies (e.g., *Apis mellifera*, *Bombus terrestris*), intercolony parasitism performed by a subspecies (*Apis mellifera capensis*), and intercolony intraspecific parasitism in queenless colonies (e.g., *A. florea*, *Apis cerana*).

Different defensive mechanisms have been described for each interaction. With regard to intracolony worker reproduction, the host reproductive female as well as her brood produce pheromones that inhibit ovarian development in the worker caste (e.g., Ratnieks 1988; Barron et al. 2001).

Also, once the parasitic egg is laid (either intracolony or intercolony), the colony's worker force usually recognizes and destroys them (Ratnieks 1988), a response that is favored by kin selection (Ratnieks 1988; Barron et al. 2001). This behavior, termed "worker policing" usually involves removal (commonly by eating) of worker-laid eggs, which smell different from those laid by the queen (Ratnieks and Visscher 1989). However, intracolony worker-laid eggs are not always destroyed; bumble bee workers are permissive about egg dumping due to their high genetic relatedness to one another (Beekman and Oldroyd 2008).

Another exception to worker policing is the case of Cape honey bees (*Apis mellifera capensis*), where eggs laid by host workers (*A. m. scutellata*) are effectively policed (Martin et al. 2002) but not those laid by the parasite probably because *capensis* females lay eggs that smell like those laid by the host queen (Ratnieks 1993; 1995).

Possible aggression between host and parasite
In some other species in which hosts do not reject parasite individuals, occasionally the host drives off the parasite. There have not been described any differences in the performance of parasitism between those cases in which the parasite is rejected and those in which it is not. Thus, these data could suggest either that though a few individuals show-defensive mechanisms, the parasitism is not costly enough to expand among the host population, or that the parasitic rate is increasing within the population and parasitism costs are also rising making defensive mechanisms evolutionarily worthwhile.

One of the animal taxa in which some species show this behavior is teleost fish, where the male often stays at the nest defending the eggs. Guarding is a very costly trait, as shown by the reduction in body mass of those males that engage in intense territorial defense of their nests (e.g., van der Berghe 1988; Ota and Kohda 2006). Paternal males experience higher energy costs than non-paternal ones (van der Berghe 1988). Parasitic male fish may spawn within a territory defended by the host male in order to fertilize some eggs there. The eggs fertilized by a male parasite will be reared and defended by the territorial male until they hatch.

Different reproductive strategies related to morphological and physiological specializations have been described in teleost fishes (e.g., Mori 1995; Ota and Kohda 2006). Territorial males attempt to gain access to female gametes through courtship and by trying to monopolize as many females as possible (Taborsky 1998). These males are sometimes parasitized by other males in 2 different ways. Smaller, inferior rivals cheat the parental male via satellite behavior: involving younger males that also participate in spawning or by sneaky behavior: in which males dart in when territorial males are spawning and release their own sperm (e.g., in *Telmatochromis vittatus*, Ota and Kohda 2006; *Lepomis macrochirus*, Gross and Charnov 1980; *Neolamprologus furcifer*, Taborsky 1998). Alternatively, larger males, known as pirates, invade the nest, spawn and leave (e.g., in *Symphodus tinca*, van der Berghe 1988). Territorial males may also steal fertilizations from neighboring territorial males, although this has only been reported in the centrarchid *Lepomis marginatus*, in which other parasitic morphs are absent (Mackiewicz et al. 2002). As defensive behavior before the performance of the parasitism, the host could fight off the intruder (e.g., Taborsky et al. 1987; van der Berghe 1988; Baba and Karino 1998; Taborsky 1998; Ota and Kohda 2006). Furthermore, when the parasitism has already been performed, males could stop care by completely cannibalizing clutches that contain a mix of self-sired and foreign-fertilized eggs (Neff 2003b; Rios-Cardenas and Webster 2005; Frommen et al. 2007). Although these strategies in fish have historically been described as alternative reproductive strategies (Krebs and Davies 1993), we should not ignore their intraspecific parasitic component (e.g., Taborsky 1997). In these cases, parasitic males obtain a reproductive benefit without suffering the costs associated with guarding.

Contrarily to fish, in some species, the offspring need to be fed by their parents after birth or hatching. Almost all endothermic parents face the energy-costly behavior of both feeding their offspring and keeping them warm, which constrains their reproductive success (Clutton-Brock 1991). In some cases, parasitic offspring have developed a "food

stealing strategy" that requires host parents to do more work to help their own young develop fully or else find that their genetic offspring suffer underdevelopment. Parasitic interactions of this sort can occur intraspecifically. For instance, in more than 100 mammalian species, neonates have been reported to suckle milk from females that are not their genetic mothers (Riedman 1982). However, alloparental care usually benefits close kin and has been reported mainly in communal breeding species, where it may generate inclusive fitness benefits for the "parasitized" female (Roulin 2002). But alloparental care has also been reported from noncommunal breeding species and in these cases, the behavior has been associated with mothers who have lost their own offspring or it may reflect the parasitic behavior of some young (Packer et al. 1992). Obviously, foster offspring will always benefit from receiving milk from foster mothers, so natural selection for juveniles that try to steal milk from nonmothers is easily explicable when juveniles are rarely punished for allosuckling (e.g., Roulin 2002; Zapata et al. 2009). In fact, high levels of milk theft by parasitic infants have been reported in several species (Murphey et al. 1995; Zapata et al. 2009). The milk theft by the allosuckler (parasitic offspring; Packer et al. 1992) costs the host female a reduction of available nutrients for her own offspring as well as reducing her future reproductive success (Roulin 2002). Allosuckling is less costly when the host female has lost all her offspring because she needs to evacuate the nonconsumed milk (Wilkinson 1992). Important benefits to the allosuckler have been described in the forms of an extra milk intake (Packer et al. 1992) and the acquisition of immunological compounds (Roulin and Heeb 1999). Exploited females frequently behave aggressively against unrelated offspring that are trying to allosuck them, which can be considered a defensive strategy (Roulin and Heeb 1999).

With counteradaptation

In other cases, the host has developed efficient defensive mechanisms. Thus, the parasite can either change host or react against these defensive mechanisms beginning a process of coevolutionary arms race (Dawkins and Krebs 1979). We can find an example of arms race interaction in those cases of parasitism where the parasite has developed a camouflage that avoids to be recognized by the host while performing parasitism. According to the arms race theory, we would expect the development of an adaptive counterdefense by hosts, which have been reported in most occasions. For instance, in some social Hymenoptera, females can usurp other females' nests. These parasitic females may be either those unable to find their own colony or females that have lost their colony, as observed in the genus *Polistes* (Cervo 2006). During usurpation, a parasitic female enters a host colony of either the same or different species (interspecific parasitism, see below) and kills the host reproductive female (e.g. Hölldobler and Wilson 1990; Cervo 2006). In consequence, no more host workers are produced and the colony gradually becomes a mixed colony until finally only the brood of the usurper is present (Hölldobler and Wilson 1990). Although the parasite obtains benefits from the host only relatively briefly, during the first stages of colony foundation, the host suffers major costs because the original queen and her workers die without producing reproductive offspring.

When the parasitic female enters a colony, the host workers may recognize her via chemical cues and attack her (Lenoir et al. 2001), but in most cases, the parasites have evolved chemical mimicry of the host (e.g., Dettner and Liepert 1994; Lenoir et al. 2001) and are not attacked by host workers.

Interspecific nest usurpation is common (e.g., Cervo 2006), although the parasite's behavior and host defenses are similar to those seen in intraspecific cases. When *Polistes nimphus* enter the colonies of *Polistes dominulus*, they stroke their abdomens on the nest surface, saturating the colony with their odor (Cervo et al. 2004).

Contrary to usurper reproductive females, inquiline ones share the queen chamber with the host reproductive female (e.g., in *Advenathrips inquilinus* [Thysanoptera: Phlaeothripidae]; Morris et al. 2000); *Ectatomma tuberculatum* (Hymenoptera: Formicidae; Hora et al. 2005); *Teleutomyrmex schneideri* (Hymenoptera: Formicidae; Hölldobler and Wilson 1990)). Once inside the colony, the parasitic female stays at the host queen chamber (e.g., Hölldobler and Wilson 1990; Hora et al. 2005), which is impregnated with the host queen's odor, with the consequence that the intruder is not attacked by the workers (e.g., Fisher 1987; Hora et al. 2005). The parasitic female begins to lay eggs that workers carry to the brood chambers as they do with the queen's offspring. The host colony soon becomes a mixed colony in which host workers perform all of the tasks (e.g., Fisher 1987; Hölldobler and Wilson 1990). The costs of this parasitism are very high as host workers have to feed and care for a nonrelated reproductive female and all her reproductive offspring. Sometimes, inquiline species produce individuals of the worker caste, but when this is the case, these workers are few and unproductive. Other inquiline species have lost the worker caste entirely and only produce reproductive offspring (Hölldobler and Wilson 1990).

As in some cases of usurpation (see above), inquiline females usually mimic the chemical signature of the host colony to gain entry to the colony (e.g., Lenoir et al. 2001), but subsequent suffusion with the host queen's odor is necessary. For example, workers of the bee *Psithyrus* sp. (Hymenoptera: Apidae) eject parasitic females in the absence of a host queen (Fisher 1987).

Parasite and host meet with aggression

In all these interactions, hosts try to fight off the parasite; thus herein, we have into consideration if the host is able to differentiate between own and foster offspring and consequently drive them off the nest or are not able to differentiate foster offspring and accept them as own.

Without offspring recognition

For many species, the nests themselves are a valuable resource requiring a large investment of both time and energy (Collias and Collias 1984; Field 1992a) as well as, sometimes, expensive materials (Brockmann 1993). In some cases, both host and parasite fight for the nest, which constitutes a valuable resource that mainly provides protection to the offspring. In these cases, the offspring is not involved while parasitism occurs, thus, no offspring recognition have been developed.

Birds commonly fight over nest boxes or near cavities at the beginning of the breeding season as a consequence of male competition. However, nest stealing between different bird species has rarely been reported. Barrios (1993) observed individual white-rumped swifts (*Apus caffer*) stealing nests from red-rumped swallows (*Hirundo daurica*). Similarly, Prokop (2004) described 40% usurpation of new black-billed magpie (*Pica pica*) nests by Eurasian kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*) in an untypical population where competition for nest sites was very high because magpie nests offered the only suitable nesting places.

In other cases, the offspring is involved in the parasitism but recognition has not evolved. For instance within eusocial Hymenoptera, slavery is a form of ant social parasitism in which the slave-making species periodically need to raid nearby host colonies to kidnap pupae and enslave the workers when these hatch (Hölldobler and Wilson 1990). To enter the host colony, parasitic species can mimic the host chemical profiles (Brandt et al. 2005) or actively produce specific allomones (chemical

weapons) that manipulate the behavior of the host species (Topoff et al. 1988; D'Ettorre et al. 2000; Mori et al. 2000a, 2000b). Some of these allomones protect a parasite queen from host aggression; others play the role of "propaganda substances" that induce attacks against ants that are marked with it (Regnier and Wilson 1971; Allies et al. 1986). Once the raid finishes, slave workers care for and feed the parasitic soldiers and pupae. As one set of host workers ages, parasitic soldiers raid another nest to restore the worker force.

As expected according to the framework of the coevolutionary arms race theory, under such deleterious parasitic consequences, host colonies have developed defenses against parasitic workers. Soldier workers congregate at the nest entrance where they bite and sting parasite workers, even killing them (e.g., Foitzik et al. 2001). A coevolutionary arms race has been reported for the slavemaker *Protomognathus americanus* (Hymenoptera: Formicidae) that mimics its hosts' cuticular profile (*Leptothorax longispinosus*; Hymenoptera: Formicidae). The host species has, in turn, evolved specific recognition abilities, which it seasonally adjusts (Brandt et al. 2005). Also in agreement with the coevolutionary arms race theory, Bauer et al. (2009) described a local coadaptation in the *Harpagoxenus sublaevis-Leptothorax sp.* (Hymenoptera: Formicidae) slave-parasite ant system. In contrast, Zamora-Muñoz et al. (2003) found no evidence of an arms race within the *Proformica longiseta-Rossomyrmex minuchae* (Hymenoptera: Formicidae) slave-parasite ant system. These authors reported that the slaves showed low aggression toward their social parasites. This could be because as the host species increases its defense, the parasites increase the intensity of its attack, implying a "mafia system," as described by Soler et al. (1998). Thus, the study by Zamora-Muñoz et al. (2003) suggests a different evolutionary direction in which the arms race would reach an evolutionary equilibrium (Zahavi 1979; see GENERAL DISCUSSION).

With offspring recognition
In some other parasitic interactions, the costly (see GENERAL DISCUSSION) behavior of offspring recognition has been developed, which drastically decrease parasitism rate.

One of these interactions is when the nestlings of many bird species themselves abandon their own nest at the end of their nestling period and move to another nest or nesting territory (Riedman 1982). This site-switching behavior is especially frequent intraspecifically, mainly in semiprecocial species of the orders Charadriiformes (Alcidae, Sternidae, and Laridae) and Sphenisciformes (e.g., Pierotti 1991; Saino et al. 1994; Jouventin et al. 1995; Brown 1998). It also occurs in altricial species of the order Ciconiiformes (Ardeidae, Ciconiidae) (Milstein et al. 1970; Redondo et al. 1995), Falconiformes (e.g., Bustamante and Hiraldo 1990; Donázar and Ceballos 1990, Kenward et al. 1993; Tella et al. 1997; Gilson and Marzluff 2000; Arroyo and García 2002), and Strigiformes (Roulin 1999; Penteriani and Delgado 2008). Site-switching behavior is more frequent when population density is high (Bustamante and Hiraldo 1990, Donázar and Ceballos 1990, Kenward et al. 1993), and sometimes can occur during the post-fledging period of dependence (known as brood-switching) (Penteriani and Delgado 2008).

Traditionally, the ornithological literature has treated nest-switching behavior as adoption behavior by foster parents. Here, we consider this behavior to be parasitism by chicks because most studies have found that it is the nest-switched chick who gains by moving to a new nest (see GENERAL DISCUSSION), although Lengyel (2007) reported a benefit of nest-switching in avocets, where nests that adopted chicks were more successful than those of non-adopting parents where the risk of predation was high.

As commented above, eusocial Hymenoptera (ants, some wasps, and bees) are vulnerable to parasitic laying by individual workers (Oldroyd 2002). Beekman and Oldroyd (2008) also described intercolony intraspecific parasitism (worker drifting) (e.g., *B. terrestris, Apis florea*) as worker parasitism. In worker drifting cases, the parasite takes advantage of the fact that failures in nest mate recognition by guard workers are not uncommon. For example, the recognition failure rate in honey bees is 10–50% (Downs and Ratnieks 2000). When either intracolony or intercolony parasitic eggs are laid, the colony's worker force usually recognizes and destroys them (Ratnieks 1988), a behavior termed worker policing, which has been discussed above.

On the other hand, the clearest cases of parasitism occur where the secondary female totally abandons a nest, as happens with burying beetles *Necrophorus* spp. (Coleoptera: Silphidae). These insects exhibit highly elaborate parental behavior that includes the burial and preparation of a small vertebrate carcass: by removing fur or feathers, burying the carrion, and depositing anal secretions on it that prevent rapid decay. The adults also protect and feed their offspring directly until the larvae leave the carcass to pupate in the soil (Müller et al. 1990). When 2 females find the same small carcass they fight for it. The winner prepares the carrion and oviposits in the surrounding soil, but the excluded female often also oviposits nearby (Wilson and Fudge 1984; Müller et al. 1990). After hatching, parasitic larvae move to the host's buried carcass where, if successful, they will be fed and guarded by the host parents (Müller and Eggert 1990; Müller et al. 1990). However, if parasitic larvae arrive at the carcass more than 20 h after the host's eggs have hatched, the host parents are able to discriminate and cannibalize them (Trumbo 1994).

But it is in birds where the recognition of foster offspring has been studied in more detail. Intraspecific brood parasitism is widespread in birds, having been documented in 236 avian species (Yom-Tov 2001), being particularly common among precocial birds such as waterfowl. The coevolutionary arms race between members of the same species is not well developed because host defenses based on foreign egg recognition are much rarer than in cases of interspecific parasitism (Davies 2000; see below). Firstly, the eggs of conspecific females are very similar in appearance, which makes egg-recognition ability very unlikely to evolve. Secondly, the costs imposed by intraspecific brood parasitism are much lower than in obligate interspecific avian brood parasitism (see below). As a result, selection pressures are not strong enough for elaborate host defenses to evolve. More detailed information on intraspecific brood parasitism can be found in several reviews (e.g., Petrie and Møller 1991; Johnsgard 1997; Davies 2000).

About 1% of bird species are known to be obligate brood parasites and they are included in 4 different orders: Cuculiformes, Passeriformes, Piciformes, and Anseriformes (Davies 2000). Interspecific brood parasitism has evolved independently 7 times in birds (Sorenson and Payne 2002). These obligate avian brood parasites impose significant costs on their hosts. In particular, brood parasitic chicks frequently evict or outcompete host chicks, usually destroying most of them. Furthermore, very often, parasitic chicks are larger than host chicks and thus elicit more intensive parental assistance from host parents for a longer time than that provided to young in nonparasitized nests (Johnsgard 1997; Davies 2000). These costs, and the fact that the breeding success of the parasite is maximized when the breeding success of the host is zero (Rothstein 1990), generate very strong selective pressures that favor the development and rapid spread of defensive adaptations and counteradaptations in this system. Indeed, coevolutionary arms races exist at all stages of the

breeding cycle: before laying and during incubation (Johnsgard 1997; Davies 2000; Soler JJ and Soler M 2000) and even during the nestling period (see a review in Soler 2009). More detailed information on interspecific brood parasitism can be found in several reviews (e.g., Rothstein 1990; Johnsgard 1997; Davies 2000).

GENERAL DISCUSSION

Parasitic interactions involving parental care are widely distributed within the animal kingdom. Throughout this review, we have explored a great variety of cases where parental care provided by parents to their offspring is parasitized by other unrelated young. The variability in both parasitized resources and animal taxa implies that the costs incurred by the victims of parental-care parasitism and the strategies used by the parasites are highly variable.

We have described a new term, parental-care parasitism, and have presented a new classification that resolves an important problem of imprecise terminology. Hitherto, such parasitic behaviors have been described by such terms as reproductive parasitism, brood parasitism, kleptoparasitism, kleptobiosis, and social parasitism. Although the boundaries between different types of interspecific interactions are indistinct, we believe that this new classification will be useful and instructive because it assists our understanding of the concepts involved. Parental-care parasitism is defined as "an interaction in which an individual (the parasite) obtains reproductive benefits while reducing or completely eliminating its own costs of parenting by exploiting any type of offspring care provided by other individuals (the hosts)." This definition is more general and includes all the terms given above. Parental-care parasitism does not necessarily imply that hosts have to rear parasitic offspring, diverting resources away from their own young. That is the meaning of the most generally used term, brood parasitism, which should only be applied to those cases where brood parasites fool hosts into raising their parasitic young.

We here offer a novel insight considering nest-switching behavior to be a form of parental-care parasitism promoted by the young themselves rather than comprising adoptions by foster parents, as it is often regarded in the ornithological literature. This point of view, which has previously been suggested by some authors (Pierotti and Murphy 1987; Kenward et al. 1993), is based on several observations. Nest-switching chicks are usually the younger members of large broods and they move to nests with younger and/or fewer chicks, where they can obtain more food than in their natal nest, thus boosting their probability of survival (Hébert 1988). Also, when foster chicks are accepted, the host parent's fitness is reduced (e.g., Saino et al. 1994; Brown 1998) because parents have to work harder to feed the increased number of chicks (Carter and Spear 1986; Saino et al. 1994; Brown 1998). Chick recognition capacity (see below) by adults has evolved in many colonial and precocial or semiprecocial species within the Charadriiformes (i.e., families Alcidae, Sternidae, and Laridae) and Sphenisciformes (see a review in Soler 2000), where nest-switching is common but no such abilities have been documented for members of the Ciconiiformes, Falconiformes, and Strigiformes (Penteriani and Delgado 2008).

Helping relatives can increase a worker individual's inclusive fitness because it is collaborating in the production of offspring by a close relative and thus transmitting its own genes to the next generation (Hamilton 1964). The workers of many wasp, bee, and ant species have ovaries and could lay unfertilized eggs, which would give rise to males. Thus, it should not be surprising that they would try to produce descendants of their own. We have classified this worker egg-laying behavior as a case of parasitic parental care in spite of the fact that workers are also genetically related to other workers as well as to the queen. However, it has recently been emphasized that the degree of kinship that exists within colonies in eusocial insects is much lower than previously believed (Ratnieks and Wenseleers 2007) because queens are quite often fertilized by several males and, in many species, there is more than one queen in each colony. Thus, workers may be expected to favor those offspring to whom they are most closely related genetically (Hannonen and Sundström 2003). Consequently, as workers do not necessarily share the same mother and father, they are less related to their sisters' offspring than to those of their mother. Kin selection thus favors investing in the male-producing eggs laid by the queen rather than in the male eggs laid by other workers (Bonckaert et al. 2008). Thus, laying workers can be considered parental-care parasites that are trying to get other workers to care for their own eggs instead of those of the queen, which would bring the latter workers greater genetic benefits.

Indiscriminate care that results in providing energy-costly resources to unrelated offspring results in a reduction of the parents' fitness and in their future fecundity (Clutton-Brock et al. 1989; Johnsgard 1997; Huber et al. 1999; Davies 2000; Koivula et al. 2003). Consequently, parental investment theory predicts that parents should discriminate between their own and unrelated offspring, avoiding parental investment in the latter. For instance, in several species of fishes, it has been reported that males stop care by completely cannibalizing clutches that contain a mix of self-sired and foreign-fertilized eggs (Neff 2003b; Rios-Cardenas and Webster 2005; Frommen et al. 2007). Also, in avian polyandrous species, beta males provide parental care according to their certainty of paternity (Davies 1992; Whittingham and Dunn 1998). However, the prediction that parents should discriminate between their own and unrelated offspring is only sometimes fulfilled.

The ability to discriminate unrelated offspring can be accomplished through visual, tactile, acoustic, olfactory, or gustatory signaling systems or a combination thereof (Sherman et al. 1997). It has been only reported regularly in 2 groups of species; in those living in communal crèches or groups (Balcombe 1990; Aubin and Jouventin 1998; Aubin et al. 2000; Insley 2000; Charrier et al. 2003; Searby and Jouventin 2003; Neff 2003a; Jesseau et al. 2008; Li and Zhang 2010) and in those that breed in dense colonies with nests close together, which allows hungry chicks to move from their nests to those of neighbors (Buckley PA and Buckley FG 1972; Beecher et al. 1981; Jouventin and Aubin 2002; Searby et al. 2004).

Also in those species that are regularly exploited by brood parasites, parents are able to discriminate and reject parasitic eggs (reviewed in Rothstein 1990, Johnsgard 1997; Davies 2000) and sometimes also parasitic chicks (Grim et al. 2003; Langmore et al. 2003; Soler 2009).

In solitary breeding species that are not exploited by brood parasites, indiscriminate care of newborn offspring is not a problem because parents are only likely to encounter their own offspring in their nest or burrow and an ability to discriminate unrelated offspring would not provide any advantage. The selective pressures favoring the evolution of discrimination behavior that can be costly (see below) do not exist in such circumstances.

It can thus be stated that, as a general rule, offspring discrimination has evolved only in those species in which the probability of being exploited by unrelated offspring is high. However, the lack of discrimination ability entails the risk of being parasitized by parental-care parasites, and the ability to recognize offspring would have obvious advantages to parents because it would reduce the amount of care provided to unrelated offspring. Therefore, the lack of discrimination ability may seem to be a maladaptation because parents fail

to act in the interest of their genes. However, there also exist risks related to offspring discrimination. Two main types of costs have been described: recognition errors, the risk of mistakenly rejecting or destroying some own eggs; and rejection costs, when parasitized individuals accidentally break their own eggs while trying to eject a parasitic egg or desert the nest or brood in response to the presence of one or more unrelated offspring (Rothstein 1990; Davies 2000; Martín-Vivaldi et al. 2002). Clearly, the costs of discrimination could actually counteract the benefits of refusing to care for parasitic offspring.

Different situations have been described for different host species or populations, which can be explained using the framework of coevolutionary arms race theory (reviewed in Lotem and Nakamura 1998). Some frequently parasitized species lack offspring discrimination behavior, and this usually is considered to be the consequence of an evolutionary lag (genes responsible for discrimination have not yet appeared). Also, some populations are rejecters while other populations of the same species are acceptors. Furthermore, rejecter and acceptor individuals frequently coexist in the same host population. These last 2 situations arise because the relationship between the costs and benefits of rejection behavior does not favor the rapid spread of the genes responsible for offspring discrimination, a circumstance addressed by the evolutionary equilibrium hypothesis (Rothstein 1990; Davies et al. 1996; Lotem and Nakamura 1998).

As we have seen, offspring recognition has only evolved in species that are exposed to a high risk of being exploited by alien offspring. This implies that absence of discrimination should be the ancestral state. Because discrimination is costly, in the absence of the risk of being exploited by young individuals that are not their genetic offspring, natural selection would penalize discriminating parents because their breeding success would be lower than that of nondiscriminators. In this situation, the most adaptive strategy for a parent is to follow a simple behavioral decision-making rule (rule of thumb): to care for any offspring placed in its nest. This rule of thumb has been demonstrated to underlie the observation that most common cuckoo hosts are not able to discriminate against the very different and huge common cuckoo chick (Davies 2000).

There are 2 other adaptive strategies related to parental care that can be exploited by parental-care parasites for their own benefit. As parental investment theory predicts, parents should adjust their parental investment to brood quality and the reproductive value of their offspring (Trivers 1972; Montgomerie and Weatherhead 1988; Clutton-Brock 1991). Consequently, parents should favor larger broods (an indicator of brood quality) and, within a brood, offspring of larger body size (an indicator of offspring quality).

Larger broods have a higher reproductive value than smaller ones and it has been found that parents' readiness to care is higher with larger broods (Magnhagen and Vestergaard 1993; Lissåker et al. 2003; Lissåker and Kvarnemo 2006). This suggests a clear advantage for parental-care parasites because if a female adds its eggs to the existing clutch of the foster parents or some parasitic young join a brood that is being cared for by those parents, these enlarged parasitized clutches or broods will provoke an increase in parental investment and a decrease in the readiness to reject the parasitic offspring. For example, male sand gobies (Pomatoschistus minutus) usually recognize their own clutches and, in an experimental study, Svensson et al. (2010) found that in the few cases where males chose to take care of foreign nests, it was a larger clutch size that influenced their parenting decisions.

Larger offspring are better competitors for resources and have a higher probability of survival (Price and Ydenberg 1995; Sogard 1997; Cotton et al. 1999; Bashey 2008). Further-more, it has frequently been reported that parents preferentially feed larger young (Rivers 2007; Smiseth et al. 2007). For example, larvae of the burying beetle (Nicrophorus vespilloides) can feed themselves from the ball of carrion prepared by the parents for them, but larger larvae additionally receive processed carrion regurgitated by their parents (Smiseth et al. 2007). This also applies with most altricial bird species, the usual hosts of avian brood parasites, where the latter take advantage of this foster parent strategy by usually parasitizing species smaller than they themselves are (Rothstein 1990, Davies 2000). Moreover, where an avian brood parasite uses host species of variable size, as with some cowbirds (Icteridae), parasitic chicks are quite successful with hosts that are smaller or that hatch later (Robinson et al. 1995; Dearborn 1998) but fare poorly with large- and/or early-hatching hosts (Lichtenstein 1998; 2001).

Finally, the concept of tolerance can help to explain the fact that parents waste resources caring for unrelated offspring much more frequently than predicted by the coevolutionary arms race theory. As recently emphasized, victims in antagonistic interactions have 2 means of defense against their enemies. One is resistance, which has a direct negative effect on the enemy and selects for counteradaptations (the basic argument of the coevolutionary arms race theory, see above). The other is tolerance, the ability to minimize the fitness impact of enemy attacks (Svensson and Råberg 2010), which does not provoke selection for counteradaptations, giving rise to a kind of coevolution that will result in stable equilibrium instead of a continuous arms race. The concept of resistance implies that in a continuous coevolutionary arms race, some of the interacting species could become extinct, which means, in the case of parental-care parasites and their hosts, that the frequency of broods including unrelated offspring should be low. On the other hand, the concept of tolerance—which has been widely considered in plant studies (Rausher 2001; Svensson and Råberg 2010) but has been completely neglected in the animal literature until recently (Restif and Koella 2003; Svensson and Råberg 2010)—involves reducing antagonistic coevolution, which implies that in many parental-care parasite-host systems, a state of evolutionary equilibrium could be reached, and so mixed broods including unrelated offspring would be expected much more frequently.

CONCLUSIONS

We have reviewed for the first time different kinds of parental-care parasitism in a great variety of animal groups that live in different ecological conditions, which could affect the cost-benefit balance of each parasitic interaction. Furthermore, we have integrated them within a new classification of parental-care parasitism based on behavioral trends, which will allow to a more easy comparison of the same parasitic interactions in different species, genders, families, or even orders.

The inability to discriminate between own and alien offspring found in some species, some populations of the same species and some individuals within the same population, can be explained according to coevolutionary arms race theory as a consequence of 1) the genes responsible for the rejection behavior not yet having appeared (the evolutionary lag hypothesis) or 2) the relationship between costs and benefits not yet having favored further spread of those genes (the evolutionary equilibrium hypothesis).

Because discrimination is costly, the fact that unrelated offspring succeed in being accepted by foster parents is because the most adaptive strategy for parents is to follow simple rules of thumb (to care for any offspring placed in my nest, to care more intensely for larger broods and for offspring of larger

body size), which are successfully exploited by parental-care parasites.

The concept of tolerance, another mechanism by which victims defend themselves against their enemies, also explains the fact that parents care for unrelated offspring much more frequently than coevolutionary arms race theory predicts. Tolerance does not provoke antagonistic coevolution, which implies that in many parental-care parasite–host systems, a state of evolutionary equilibrium would be reached, so that broods including unrelated offspring will be encountered more frequently.

Finally, the information provided about most cases of parental-care parasitism reported in the literature is incomplete and scarce. Much of what has been reported relies on unreplicated studies. Thus more empirical and experimental studies are needed in order to gather the missing information. Four important directions for future research are: 1) determining the frequency and characteristics of parental-care parasitism in different populations of reported parental-care parasite–host systems, 2) experimental assessing of the relationship between costs and benefits in each system, 3) experimental testing of the offspring discrimination capacity of parents in host species and in their closest relatives, and 4) assessing the relative importance of the 2 means of defense used by hosts against their parental-care parasites (resistance and tolerance) in each system.

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