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3 **Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on**
4 **participant mobility, of the conditions promoting the evolution of kleptoparasitism**
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16
17 **Running head:** Evolution of kleptoparasitism

18

1 **ABSTRACT**

2 Understanding of the conditions encouraging the evolution of kleptoparasitism has been
3 limited by the preponderance of attention focused on a limited number of taxa (predominantly
4 birds). However, most animal taxa contain kleptoparasitic members. In many ways, adult birds
5 are aberrant because most are acrobatic, capable of three-dimensional movement, and steal from
6 hosts that are capable of similar feats. The mobility of kleptoparasites and their hosts falls along
7 a continuum, with the acrobatic birds at one end and sessile hosts and kleptoparasites at the
8 other. Considering sedentary systems requires amendments to the criteria previously outlined as
9 necessary for kleptoparasitism. Kleptoparasitic interactions between agile participants are
10 ephemeral, involve numerous hosts over the lifetime of the kleptoparasite, and usually rely on
11 vision. Large concentrations of hosts and large, high-quality food items are important in mobile
12 systems. By contrast, the long-term, intimate associations of sedentary interactions demand that
13 the host not consume the kleptoparasite's offspring and that the host must either have a longer
14 life cycle than the kleptoparasite or be located in aggregations that have staggered life cycles (so
15 the kleptoparasite can move to a new host when the original host dies). Expanding studies of
16 kleptoparasitism to other taxa will differentiate between the selective pressures and evolutionary
17 responses that are universal among kleptoparasitic symbioses and those that are restricted to
18 certain groups.

19

20 **Keywords:** avian-competition-feeding-invertebrates-mobility-dependent traits-theft

1 INTRODUCTION

2 Kleptoparasitism, a form of competition that involves the stealing of already-procured
3 items, is one of the most common types of exploitation between animals (Rothschild & Clay
4 1952, Brockmann & Barnard 1979, Barnard 1984a, Vollrath 1984). Historically, most
5 kleptoparasitic studies have focused on birds, but the prevalence of this behavior is much
6 broader in its taxonomic distribution (Table 1). The preponderance of studies reporting
7 kleptoparasitism in birds versus other taxa likely reflects research effort and visibility more than
8 a true pattern in nature. Herein, I provide a brief survey of kleptoparasites across the animal
9 kingdom as evidence of the ubiquitous nature of this behavior. The following collection of
10 examples is not an exhaustive list of kleptoparasites, but rather a variety of examples to
11 demonstrate that this behavior is widespread, both taxonomically and ecologically. For many of
12 the examples listed, extensive quantitative studies have not been performed. Instead, short
13 descriptions of the interaction have been published, often as part of a larger work on a subject
14 other than kleptoparasitism. My hope in compiling this list is to encourage quantitative,
15 experimental and comparative studies of kleptoparasitic interactions.

16 The conditions traditionally identified as promoting the evolution of kleptoparasitism are
17 skewed by previous heavy reliance on avian examples, many of which involve highly mobile
18 kleptoparasites and hosts. Some of these requirements do not hold true in more sedentary host-
19 kleptoparasite associations (which are common). While many studies have examined
20 evolutionary responses to selective pressures exerted by predators on prey and internal parasites
21 on hosts, these impacts are rarely explicitly recognized for kleptoparasitic interactions.
22 Kleptoparasitism can be a major driving force in the evolution of the morphology and behavior
23 of the participants, as hosts and kleptoparasites respond to the selective forces exerted by each

1 other. Using Brockmann and Barnard's (1979) and Paulson's (1986) previous hypotheses based
2 on birds, I compare and contrast the traits of kleptoparasitic interactions in systems that involve
3 acrobatic players (such as in many birds) with those with movement-limited participants to
4 assess which conditions critical to the evolution of kleptoparasitism are the same in both groups.
5 By considering interactions in previously unstudied taxa, scientists can identify group-specific
6 and general rules governing kleptoparasitism.

7

8 **The definition of "kleptoparasitism"**

9 Kleptoparasites steal food that is either already in the host's possession, or for which the
10 host has expended energy and capture by the host is imminent. Thus, a hawk that intercepts and
11 eats a mouse that is closely chased by a cat, or a marine snail that captures food particles from an
12 oyster's feeding currents may both be considered kleptoparasites. The kleptoparasite must incur
13 a benefit and the host must be negatively affected by the loss of food (otherwise the interaction
14 should be designated kleptobiosis; Vollrath 1984). If the thief steals food items normally not
15 ingested or otherwise used by the host—waste products (Yamahira and Yano 2000, Morton and
16 Jones 2001) or food too small to be consumed by the host (Vollrath 1984)—or removes food
17 items from an aggregation larger than the host could reasonably subdue and consume (e.g.,
18 animals sharing a large, rich food patch), then the interaction is not kleptoparasitism, as the
19 "host" animal does not incur an energetic cost via loss of food. Kleptoparasites do not injure the
20 hosts in any direct way other than through loss of nourishment.

21 Kleptoparasitism is a form of competition, and should specifically refer to interactions
22 between unrelated individuals (either inter- or intra-specific interactions). Individuals that steal
23 food from relatives (parents, siblings) are not kleptoparasites because increased indirect fitness

1 may overcome the reduction in direct fitness. Kleptoparasitism can be either obligate (the sole
2 obtainment mode of the animal) or facultative (one of a number of modes). Kleptoparasitic
3 interactions vary in the interim of time between theft and discovery, and in the degree of
4 interactions between the thief and owner. Some kleptoparasites interact directly with the host,
5 forcibly taking food despite host attempts at defense (e.g, skuas from puffins, hyaenas from wild
6 dogs; Furness 1987, Carbone et al. 1997). In other cases, kleptoparasites steal resources from
7 ignorant owners (termed “stealth kleptoparasitism” by Giraldeau & Caraco 2000; e.g., *Argyrodes*
8 spiders stealing food while the host spider is subduing another victim).

9 The root “klep-” means to hide or to steal (Guralnik 1982), so in terms of etymology,
10 kleptoparasitism should refer to the generalized theft of any resource, not just food. Authors in
11 avian systems have expanded kleptoparasitism to include the stealing of nest material
12 (Vanderwerf 1998), spatial resources (e.g., nest sites; Wood et al. 2000, Kappes 1997) and eggs
13 (to falsely advertise mating status; Perrin 1995). However, selective pressures on various
14 interactions may be very different: the loss of a meal and the loss of offspring likely incur
15 different costs. Therefore, authors must be clear as to which subset of kleptoparasitic behaviors
16 they are discussing, especially if any theft other than the stealing of food is at issue.

17 In this paper, I (1) examine the conditions promoting the evolution of kleptoparasitism—
18 which traits are common across all interactions and which are mobility-dependent, (2) briefly
19 review the wide variety of kleptoparasitic interactions (interspecific and intraspecific) in
20 terrestrial and aquatic environments, (3) examine taxa conspicuously lacking kleptoparasites, (4)
21 highlight the few instances of obligate (versus facultative) kleptoparasites, and finally, (5)
22 examine the variation in host response to kleptoparasites. I conclude by hypothesizing why

1 kleptoparasites may be underreported in the literature, and suggesting potential model systems
2 that are likely to broaden our understanding of the evolution of kleptoparasitic interactions.

3

4 **Ecological conditions promoting kleptoparasitism**

5 In their 1979 review paper, Brockmann and Barnard outlined the ecological conditions
6 encouraging the evolution of kleptoparasitism in birds (Tables 2 & 3, as indicated). Paulson
7 (1986) added to this list, again using avian examples. There has not been a comparable
8 examination of non-avian systems. Thus, it has remained unexamined whether the conditions
9 previously outlined are unique to birds, are common only among mobile participants, or are
10 universal. Examining non-avian systems, some identified conditions are common to all
11 kleptoparasitic interactions (Table 2), but others differ across taxa (Table 3). This variation
12 often can be attributed to the movement abilities of the participants (highly mobile versus
13 sedentary) rather than to habitat (e.g., aerial, terrestrial or aquatic).

14 Kleptoparasitic interactions among adult birds typically involve mobile participants, with
15 both the kleptoparasite and the host capable of rapid travel, movements, and feints in three-
16 dimensional space (Furness 1987). In contrast, although some insects are capable of acrobatic
17 flight and many planktonic animals (e.g., fish, squid, copepods) are capable of three-dimensional
18 movements, the majority of invertebrate groups are more sedentary and less agile. Many aquatic
19 animals are sessile, and even the mobile aquatic and terrestrial invertebrate hosts are usually
20 restricted to two-dimensional non-acrobatic movement (e.g., sea stars, crabs, ants and bees in
21 nests, spiders on webs). Even among terrestrial vertebrates, most do not engage in the fast-
22 paced, acrobatic interactions typical of birds.

1 Evasion and pursuit tactics by birds differ greatly from those employed by animals
2 restricted to two-dimensional (or no) movement. Highly mobile hosts can only be
3 kleptoparasitized by clinging or equally mobile kleptoparasites (Vollrath 1984). Thus, the
4 kleptoparasites of birds generally are only other birds (Brockmann & Barnard 1979, Furness
5 1987). The movement abilities of both participants have important ramifications for the
6 ecological conditions necessary to promote kleptoparasitism.

7

8 *Traits consistent across the range of mobilities* (Table 2)

9 According to Furness' (1987) food suitability criterion, the host must obtain food in such
10 a way that the parasite can steal it. This requirement should hold for movement-limited
11 associations as well as mobile ones. If food is immediately incorporated into metabolic
12 processes, a kleptoparasite has no chance to intercept it. Animals that require long prey handling
13 times, transport prey items, and those that store food (for use by themselves or their offspring)
14 risk exploitation by kleptoparasites (Vander Wall 1990, Sivinski et al. 1999). Birds in a breeding
15 colony, the most common targets of avian kleptoparasites, transport food back to chicks. Spiders
16 and hymenopterans collect food and store it for later use, thus rendering that food susceptible to
17 kleptoparasites. In rock-shore marine systems, sessile suspension-feeding animals greatly
18 outnumber mobile animals (Little & Kitching 1998). Whether these suspension-feeders collect
19 food on outstretched projections and transport it to their mouths (as in anemones, hydroids, and
20 tube-dwelling polychaete worms) or use an internal food-collecting apparatus (as in bivalves,
21 filter-feeding snails, tunicates, and brachiopods), energy is expended to concentrate a dilute
22 medium (Riisgård & Larsen 2001) and there is a time lag between food collection and digestion.
23 This time lag provides the potential for exploitation by other animals.

1 If the kleptoparasite cannot digest the food it has acquired, then it receives no nutritional
2 benefit. In birds, opportunistic kleptoparasitism most commonly occurs in mixed-species nesting
3 colonies and feeding flocks where many predatory birds forage simultaneously on the same food
4 source (Brockman & Barnard 1979, Furness 1987). In these aggregations, the likelihood that an
5 individual bird can utilize the food of nearby birds is great. Many marine kleptoparasites are
6 descended from suspension feeders and steal food from suspension feeding sedentary hosts.

7 To avoid wasted chase-time, the kleptoparasite must recognize hosts that will provide
8 suitable food resources. While birds are predominantly visually-oriented, chemoreception and
9 touch transcend the importance of vision for many invertebrates (Vollrath 1984, Morissette &
10 Himmelman 2000a). As circling vultures alert visually-oriented kleptoparasites for miles
11 (Meinertzhagen 1959), chemical cues and vibrations in aquatic systems can range far distances.
12 Because vision is not the primary sense used by many invertebrates, Brockmann and Barnard's
13 (1979) condition of "visible food" and Paulson's (1986) "open habitat" requirement and its
14 inherent corollaries do not apply explicitly in many marine and terrestrial kleptoparasitic
15 interactions. However, by slightly altering "visible food" to read "detectable food," that
16 condition now applies. Habitats allowing transmission of cues (visible, chemical, or tactile) that
17 identify hosts with food and areas through which the kleptoparasite can move are necessary to
18 allow kleptoparasitism, regardless of the identity of the participants.

19 For kleptoparasitism to be profitable, the benefit (energy gained) must exceed the cost
20 (energy expended and risk of injury from the host). An animal's ability to assess the trade-offs
21 involved in kleptoparasitism versus independent foraging is important. Some kleptoparasitic
22 spiders and the whelk *Buccinum undatum* accept a higher risk of predation for greater access to
23 food (Vollrath 1979, 1984, Rochette & Himmelman 1996, Whitehouse 1997). Other spiders

1 base host preference on the probable prey-capture rate versus the level of danger from aggressive
2 hosts (Henaut 2000).

3 Learning, with different levels of complexity, has been demonstrated in birds and
4 invertebrates (Thompson & Barnard 1984, Vollrath 1984, Alcock 2005). Both highly mobile
5 and sedentary animals that can hone their skills, fine-tune their movements and timing to that of
6 hosts, remember the benefits gained, and determine when the profits of kleptoparasitism
7 outweigh the risks, can be rewarded with high success, increasing facultative kleptoparasitism in
8 the population.

9 Brockmann and Barnard (1979) also proposed that the typical habitat of the host and the
10 kleptoparasite must be congruent, to enable the kleptoparasite to encounter potential hosts
11 frequently, especially if a new host is required after each theft. While this condition also applies
12 when both participants are sessile, it is less necessary if the host is sessile and the kleptoparasite
13 is capable of extensive movement. Then, because the host is always located in the same place,
14 the kleptoparasite could potentially spend most of its time elsewhere, moving to the host's habitat
15 only when hungry—although congruent host-kleptoparasite habitat still likely promotes
16 kleptoparasitism by reducing costs due to a decrease in required movements.

17

18 *Traits varying across the range of mobilities (Table 3)*

19 Kleptoparasitic interactions are not necessarily fleeting interactions, involving different
20 hosts for each bout. The length of time spent in kleptoparasitic interactions ranges from a few
21 minutes to kleptoparasites that spend almost their entire lives on the same host. Highly mobile
22 kleptoparasites, such as some birds, may not live in constant contact with individual hosts and
23 may participate in kleptoparasitism only at certain times of the year (Furness 1987). In contrast,

1 many invertebrate kleptoparasites form long-term intimate associations with their hosts and
2 obtain the majority of their food through the interaction. Some kleptoparasitic ants and bees
3 spend their entire lives with hosts, as they are incapable of feeding themselves (Caullery 1952,
4 Wille 1983). Some marine snails remain attached to the same host for extended periods of time
5 (sometimes months; e.g., Orr 1962, Habe 1964, Thorson 1965, Schiaparelli et al. 2000, Iyengar
6 2002a, 2004), gain the bulk of their nutrition by theft (Iyengar 2002a, Morissette & Himmelman
7 2000a), and are rarely found apart from a host except during mating season (Iyengar 2005).

8 Long-term, intimate associations demand that the parasite refrain from negatively
9 impacting the host to the extent that the host's vitality is threatened because then the
10 kleptoparasite also suffers if it cannot move to a new host. On the other hand, fleeting
11 interactions with different hosts enable the parasite to exert a large negative cost on each host.
12 Thus, opportunistic avian kleptoparasites steal up to a third of an individual host's food, whereas
13 specialist avian kleptoparasites steal less than one percent of a host's food (Furness 1987).
14 Sedentary kleptoparasites should have an even stronger dependency on the viability of a
15 particular host. Quantitative studies comparing the impacts on hosts of specialist and facultative
16 kleptoparasites in sedentary systems would be interesting, but are largely lacking.

17 Brockmann and Barnard (1979) proposed that, because an avian kleptoparasite
18 repeatedly must find new food-carrying hosts, a high density of hosts is required. Once a host
19 has been robbed, it is useless to kleptoparasites until it again forages successfully. However,
20 sessile hosts can sometimes simultaneously support multiple kleptoparasites, reducing the host
21 density needed. Moreover, movement-limited kleptoparasites often remain on the same host for a
22 significant portion of the parasite's life. Thus, as long as the kleptoparasite can find a host
23 reliably within a critical window of search time (often during larval dispersal for invertebrates),

1 the density of surrounding hosts is often irrelevant. The common correlation between particular
2 animals and habitats may assist kleptoparasites in reliably locating hosts. In this way,
3 movement-limited kleptoparasites rely on predictable host habits, just as Brockmann and
4 Barnard (1979) outlined for highly mobile systems. But the required density of hosts can differ
5 between mobile and movement-limited systems.

6 Because avian kleptoparasites are often involved in energetically expensive chases that
7 are not successful (Furness 1987), Brockmann and Barnard (1979) postulated that the hosts must
8 control large amounts of nutritious food (either held in the beak or the crop) to allow
9 kleptoparasites to obtain a net energy gain. But this stipulation is often unnecessary in long-
10 term, sedentary associations. The foraging strategies of aquatic sessile suspension-feeding
11 animals differ from those employed by mobile animals (Okamura 1990). If environmental
12 conditions are suitable, suspension feeders feed continuously rather than during short time
13 intervals (Yonge 1935), so the kleptoparasites on these hosts can steal food at any time,
14 expending little energy beyond the initial investment required to establish the interaction. In
15 systems involving bee or ant nests, spider webs, and carrion or dung resources, the food resource
16 is present for an extended period. Thus, in sedentary and sessile systems, the host must reliably
17 procure enough food to sustain the basic life function of itself and its kleptoparasites, but large,
18 high-quality individual food items are unnecessary due to a continuous, rather than intermittent,
19 food supply.

20 Additional requirements, unanticipated by Brockmann and Barnard (1979), must be met
21 to allow long-term kleptoparasitic associations between the same host and parasite. In
22 movement-limited interactions, either the life span of the host must exceed the time required for
23 the kleptoparasite to mature and reproduce (Thorson 1965) or the hosts must aggregate in

1 heterochronous assemblages, with host death staggered. If the host life-span were shorter than
2 the kleptoparasite's generation time, the kleptoparasites would soon go extinct in a habitat of
3 widely dispersed hosts, unable to move easily to a new host.

4 In long-term host-parasite relationships, the host must not consume many of the
5 kleptoparasite's offspring, either during parasite hatching or settlement, because mortality due to
6 hosts could negate any fecundity benefit gained by the kleptoparasite through increased
7 nutrition. The necessary proximity of the kleptoparasite to the feeding apparatus of the host
8 increases the danger posed to the kleptoparasite's offspring. Therefore, the kleptoparasite must
9 either leave its host to reproduce or the offspring must be immune to, or avoid, host
10 consumption. Some polychaete hosts will eat the larvae of kleptoparasitic snails residing on them
11 (Iyengar unpublished data). The departure of the snails from their hosts prior to mating and the
12 delay of returning until after the eggs hatch (Iyengar 2005) is probably an adaptation of the snails
13 to limit the consumption of young by hosts. Mobile kleptoparasites do not face the same
14 restrictions, as the nests of kleptoparasites are often distant from the raiding grounds of the
15 adults, and often the hosts are not predators of the kleptoparasite's offspring.

16

17 **Who are kleptoparasites? Interspecific kleptoparasitism**

18 *Among terrestrial animals: Birds*

19 Numerous previous works (e.g., Meinertzhagen 1959, Brockmann & Barnard 1979,
20 Furness 1987) provide thorough reviews or plentiful examples of the most-studied taxon of
21 kleptoparasites, the birds, so treatment of this group here is brief.

22 Certain avian orders, usually opportunistic feeders, contain a disproportionate number of
23 kleptoparasites, with sea birds possessing the most (Brockmann & Barnard 1979). Nearly all the

1 raptors rob each other of food (Meinertzhagen 1959). Bald eagles snatch fish from osprey
2 (Curio 1976), gulls harass diving ducks, and American wigeons rob coots of weeds (Rothschild
3 & Clay 1952, Meinertzhagen 1959). Sometimes gulls and corvids even parasitize
4 kleptoparasites (Brockmann & Barnard 1979). More rarely, birds steal food from non-avian
5 quarry (Watt et al. 1995). Passerines and hummingbirds steal food from spiders' webs
6 (Brockmann & Barnard 1979, Vollrath 1984), African thrushes and bulbuls rob driver ants
7 (Rothschild & Clay 1952, Curio 1976), and gulls and bald eagles occasionally grab food from
8 sea otters and seals (Fisher 1939, Meinertzhagen 1959, Watt et al. 1995, M. Staedler pers.
9 comm.).

10

11 *Among terrestrial animals: Arthropods*

12 Interspecific kleptoparasites are common among the arthropods, and represent the second
13 most-studied group of kleptoparasites. A review of many of the smaller dipteran kleptoparasites
14 can be found in Sivinski et al. (1999) which lists over 33 adult and 17 larval kleptoparasitic flies.
15 Facultative kleptoparasitism is widespread among hymenopterans, both in larvae and adults.
16 Maeta et al. (1996) report 26 species of kleptoparasitic bees in Japan alone. In the superfamily
17 Apoidea, kleptoparasitism has evolved independently in four families (Iwata 1976). Stingless
18 bees pillage other bees' nests, stealing pollen and honey (Wille 1983). While more than 35
19 genera of bees contain kleptoparasitic members, only four wasp genera do (Iwata 1976). Larvae
20 of the scarabaeid beetle *Aphodius rufipes* will consume the brood stores of *Geotrupes spiniger*,
21 another scarabaeid (Klemperer 1980). Mites (*Antennophorus* sp.) in the nests of *Lasius* ants
22 cling to the workers and drink droplets passed between hosts or titillate the host to induce
23 regurgitation (Wheeler 1913). The ants try to rid themselves of the parasites when the mites first

1 attach, but soon become indifferent (Wheeler 1913). Staphylinid beetles are the most common
2 kleptoparasites of ant and termite nests (Caullery 1952). Ants seek larvae of the staphylinid
3 beetle *Lomechusa strumosa* and provide them with food, even at the expense of the ant larvae, to
4 receive non-nutritive aromatic ether secretions in return (Caullery 1952).

5 "All stages of specialisation, from an independent facultative thief to a completely
6 dependent, obligatory symbiont, can be found among spiders" (Vollrath 1984: 87), and the most
7 usual hosts are web-spinning spiders. Some kleptoparasitic spiders remain on the outskirts of the
8 host's web, stealing wrapped prey from the web's center while the host spider is busy elsewhere
9 (Vollrath 1984). Other spiders (such as the obligate kleptoparasite *Curimagua bayano*) interact
10 directly with the host to steal food (Vollrath 1978). The spider genus *Argyrodes* possesses the
11 most kleptoparasitic members, or at least the most studied, and many have specialized, becoming
12 morphologically and behaviorally adapted to kleptoparasitism (Tso & Severinghaus 1998).
13 Some parasitize a wide range of hosts, with host preferences, location on the web, and level of
14 aggression towards other kleptoparasites determined by tradeoffs between prey-capture rate, the
15 ease of access to the web and the level of danger to the parasite itself (Vollrath 1979, Vollrath
16 1984, Whitehouse 1997, Tso & Severinghaus 1998, Henaut 2000).

17

18 *Among terrestrial animals: Non-avian vertebrates*

19 Herbivores may also steal food. Pikas sometimes steal haypiles, winter sustenance, from
20 neighbors (McKechnie et al. 1994, Dearing 1997). Few carnivorous vertebrates specialize in
21 kleptoparasitism, but many take advantage of easy food. Komodo dragons (*Varanus*
22 *komodoensis*; reptiles) and feral dogs kleptoparasitize each other: feral dogs chase small dragons
23 from carrion and large dragons supplant feral dogs (Auffenberg 1981). All large African

1 carnivores, except the cheetah, steal meat at times (Curio 1976). Spotted hyenas steal meat from
2 at least seven predators (lion, cheetah, leopard, wild dog, jackal, vulture and man), obtaining up
3 to 26 percent of their carcasses by scavenging (Curio 1976).

4

5 *Among aquatic animals: Arthropods, Echinoderms, and Annelids*

6 Contrary to previous statements (Pernet & Kohn 1998, Morissette & Himmelman 2000a),
7 there is a wide variety of marine kleptoparasites. The paucity of documented cases in the marine
8 realm may be due to a dearth of investigators in the field and a tendency for such interactions to
9 be mentioned in passing in the context of another topic, rather than being labeled as
10 kleptoparasitism *per se*.

11 Grenadier crabs (*Lybid tessellata*, *Polydectes cupulifera*) carry anemones in each claw
12 for defense and food gathering—if the anemone does not ingest food quickly, the crab steals it
13 (Street 1974). The crabs *Hyas araneus* and *Cancer irroratus* steal food from the asteroid
14 *Leptasterias polaris* and likely acquire a substantial part of their diet from this host (Morissette
15 & Himmelman 2000a). Porcellanid crabs and amphipods shelter under hermit crab shells for
16 protection and may snatch part of the host's meal (Telford & Daxboeck 1978, Taylor 1979,
17 Vollrath 1984). Hydroids (*Eudendrium glomeratum*) lose food to caprellid amphipods
18 (Bavestrello et al. 1996), while the ascidian *Corella parallelogramma* harbors at least eight
19 copepod species, including one (*Ascidicola rosea*) that feeds exclusively on the host's food
20 (Gotto 1957). "Inquilinism [sharing the home of another organism] merges by slow degrees into
21 parasitism, as we can see in the copepods that parasitize ascidians" (Caullery 1952: 31).

22 Within the Echinodermata, sea stars will steal food from other sea stars (Wobber 1975,
23 Sloan 1979, 1984, Morissette & Himmelman 2000a, 2000b). Some juvenile brittle stars steal

1 food from adult brittle stars and crinoids (Warner 1971, Clark 1976, Hendler et al. 1999), even
2 going so far as to reside in the bursae of the host (e.g., *Ophiomastix annulosa* within *Ophiocoma*
3 *scolopendrina*) to be within arm's reach of the host's stomach (Hendler et al. 1999).

4 Many scaleworms (Phylum Annelida) shelter in the ambulacral grooves of sea stars
5 where they can take food from the host's tube feet and stomach. *Podarke pugettensis* and
6 *Acholoë squamosa* make regular forays to their hosts' oral regions, even into the stomachs
7 (Dales 1966, Freeman et al. 1998).

8
9 *Among aquatic animals: Molluscs*

10 Despite their stereotypical slow movements, almost all known kleptoparasitic molluscs
11 are marine gastropods. *Epitonium clathratulum* (a wentletrap) sits in the mouth slit of the
12 anemone *Bunodosoma biscayensis*, and extends its proboscis into the anemone's gastric cavity to
13 feed (Den Hartog 1987). The snail responds quickly to food: within 15 minutes of an anemone
14 feeding, the snail can scale the anemone and position itself at the host's mouth (Den Hartog
15 1987). *Odostomia scalaris* removes organisms from the branchial chamber of mussels and may
16 steal food from tube-dwelling annelids (Baer 1952). The whelks *Buccinum undatum* and
17 *Kelletia kelletii* steal food from sea stars; sometimes a significant part of their diet is obtained
18 this way (Rosenthal 1971, Rochette et al. 1995, Morissette & Himmelman 2000a).

19 The kleptoparasitic snails just mentioned belong to carnivorous, scavenging or parasitic
20 families, similar to avian kleptoparasites. However, many kleptoparasitic snails exist within
21 suspension feeding taxa, especially within the family Capulidae. Unfortunately, except for
22 *Trichotropis cancellata* and *Capulus ungaricus*, little is known about the biology of capulids.

1 *Trichotropis cancellata*, a facultative kleptoparasitic marine snail, can both suspension
2 feed and steal food (Pernet & Kohn 1998, Iyengar 2002a). To steal food, the snail resides on a
3 host, often a tube-dwelling polychaete worm, and extends its pseudoproboscis between the host's
4 feeding tentacles and into the host's mouth. *Trichotropis cancellata* kleptoparasitizes at least
5 five polychaete tube-worms and one holothuroid (Pernet & Kohn 1998, Iyengar 2002b, 2004,
6 2005). The snail grows more quickly as a kleptoparasite than as a suspension feeder, and
7 significantly reduces worm hosts' growth rates (Iyengar 2002a, 2004).

8 The snail *Capulus ungaricus* is a self-sufficient suspension feeder in food-rich waters, but
9 it steals food from bivalves, snails, tube worms and brachiopods in food-poor waters (Orton
10 1949, Sharman 1956, Orr 1962, Thorson 1965, Graham 1988). To access food on a host
11 bivalve's gill, *C. ungaricus* overlaps its shell with the edge of the host, often rasping a crescent in
12 the host's shell margin (Orton 1949, Sharman 1956). Thorson (1965) suggested that juvenile *C.*
13 *ungaricus* may intercept host feeding currents but not steal food from the host's gill, but this has
14 not been fully investigated *in situ*.

15 Kleptoparasitism in other capulids has been little studied. *Capulus danieli*, *C.*
16 *sycophanta*, and *C. dilatatus* drill through the shell and mantle of host scallops to access
17 concentrated food at the labial palps and food-gathering tracts (Orr 1962, Matsukuma 1978,
18 Hayami & Kanie 1980). *Capulus subcompressus* uses its pseudoproboscis to steal food from
19 tube worms (Schiaparelli et al. 2000) and *Separatista helicoides*, always found on fan-worm
20 tubes, is believed to steal food (Okutani 1997).

21

22 *Among aquatic animals: Vertebrates*

1 Individual minkes have been known to feed predominantly as kleptoparasites, exploiting
2 the efforts of birds that concentrated prey (Hoelzel et al. 1989). Reports of piscine
3 kleptoparasites are rare (Dominey & Snyder 1988). No fish is known to be an obligate
4 kleptoparasite, but opportunistic interactions, especially between fish, occur. Groupers cause
5 foraging moray eels to drop items and blue jacks steal food from bottom-feeders (Dominey &
6 Snyder 1988). Among reef fishes, portions of a single item are commonly found in the stomachs
7 of two or more fish, suggesting that a second fish commandeered part of the predator's meal (B.
8 Shank pers. comm.), which has occasionally been witnessed (B. Tyler pers. comm.). Western
9 buffalo bream (*Kyphosus cornelii*) tend individual algal gardens, but, if the defendability of the
10 garden is low, they will also make kleptoparasitic forays into the gardens of conspecifics
11 (Hamilton & Dill 2003). Even sharks can be the victims of interspecific kleptoparasites. In an
12 aquarium, a hump-headed Maori wrasse (*Cheilinus undulatus*) rammed its head into the
13 abdomen of a juvenile whitetip reef shark, then ate the regurgitate (Garner & Mackness 1999).
14 In the Galapagos, rainbow runners (*Elagatis bipinnularus*) may obtain food from sharks in a
15 similar manner (Garner & Mackness 1999). Some fish steal food from non-piscine species:
16 cichlids in West Africa opportunistically steal food from crabs (Dominey & Snyder 1988).

17 Many more of these aquatic kleptoparasitic interactions doubtless occur, but sightings of
18 them are infrequent, likely due to the difficulty of observing natural interactions in underwater
19 environments. Additionally, quantitative studies of the costs and benefits of these interactions
20 are currently absent.

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Who are kleptoparasites? Intraspecific kleptoparasitism

Some examples of intraspecific kleptoparasitism are between young life stages, set into motion by the oviposition behavior of the parents. Burying beetles (*Nicrophorus* sp.) not only compete for food with carrion fly larvae (interspecific competition), but also face intraspecific kleptoparasitism when subordinate females oviposit near a carcass controlled by a conspecific (Trumbo 1994). The offspring of these interlopers feed on the carcass, reducing the amount of food available to the offspring of the dominant beetles (Trumbo 1994). Wuellner (1999) noted that some females of a gregarious ground-nesting bee exploit pollen stored by other ovipositing females by bringing no pollen and ovipositing in many nests.

However, most documented examples of intraspecific kleptoparasitism involve interference competition between adults. In flocks of house sparrows, some individual birds specialize in this behavior, obtaining a large part of their diet by following foragers and snatching their food (Barnard & Sibly 1981). Kleptoparasitic spiders (Vollrath 1979, 1984, Whitehouse 1997, Tso & Severinghaus 1998), water crickets (Andersen 1982, Erlandsson 1988) and frogs (in laboratory situations: *Rana pipiens* and *R. clamitans*; Boice & Williams 1971) will steal food from conspecifics.

Turtles are candidates for kleptoparasitic interactions as they spend much of their active time foraging and aggregate where food is abundant (Harless 1979). However, kleptoparasitism has never been observed in wild populations of turtles, although it has been noted in captive populations (western and midland painted turtles, box turtles, wood turtles, and red-eared sliders; Boice 1970, Harless 1979, Mahmoud & Klicka 1979, Hayes 1986, 1987). Further research is needed to ascertain the extent of kleptoparasitism in wild turtle and terrapin populations.

1 Kleptoparasitism is rarely reported, but likely common, in lizards (L. Vitt pers. comm.).
2 When prey is scarce, kleptoparasitic attempts are frequent among captive lizards (green anoles,
3 lacertid lizards, blue spiny lizards), causing individuals to retreat from conspecifics to consume
4 food (Greenberg 1976, B. Cooper pers. comm.). Kleptoparasitism is also common in groups of
5 the cordylid lizards *Platysaurus broadleyi* and *P. lilfordi* when food items are too large to be
6 consumed in a single gulp (Cooper and Pérez-Mellado 2003). In Komodo dragons, hunting is
7 solitary but fresh kills attract other lizards and kleptoparasitism is likely at all large kills
8 (Auffenberg 1981). The intraspecific feeding hierarchy insures that the largest individual
9 receives the best morsels, regardless of which lizard made the kill (Auffenberg 1981).

10 Intraspecific kleptoparasitism is common among sea otters (*Enhydra lutris*) that forage
11 between 11-13 hours per day, with fairly regular routines and peaks of activity (Love 1992).
12 Predictable habits, large aggregations, and hoarding promote exploitation (Fisher 1939, Love
13 1992). Rarely do otters fight over food; the original owner usually just forages again and
14 surfaces at a distant spot (Fisher 1939). The alpha sea otter can take food from any otter (Fisher
15 1939). Other kleptoparasites are usually adult territorial males and the victims usually females
16 with pups, although female-female and male-male kleptoparasitism sometimes occurs against
17 less-experienced or recently-injured individuals (Riedman & Estes 1988, M. Staedler pers.
18 comm.).

19 Great white sharks (*Carcharodon carcharias*) search individually for prey, but remain
20 close enough to exploit a conspecific's kill. During a five-year study in the South Farallon
21 Islands, multiple sharks were usually seen only when feeding together on a recent kill, and threat
22 displays aimed at conspecifics often occurred in these aggregations (Klimley et al. 2001).

1 As in interspecific kleptoparasitism, intraspecific kleptoparasitism can exert selection
2 pressures strong enough that individuals change feeding behaviors. Northern pike (*Esox lucius*)
3 choose smaller prey than predicted by energy budgets to lower the risk of intraspecific
4 kleptoparasitism (Nilsson & Bronmark 1999).

5

6 **Groups apparently not plagued by kleptoparasites**

7 Taxa apparently immune to kleptoparasites also provide insight into this feeding mode.
8 Toads, frogs and salamanders may allow little opportunity for food-stealing (intra- or inter-
9 specific), as they typically consume small prey in one gulp and generally lack chewing
10 abilities—which means that prey are immediately transferred to the stomach rather than
11 masticated or placed in a storage crop (K. Zamudio pers. com.). Even though they usually prey
12 on larger food items that require extended time periods to consume and digest, snakes eat at
13 widely spaced intervals. Therefore, the likelihood that a feeding snake will be challenged for a
14 food item by another animal is small (H. Greene pers. com.).

15 Crocodiles seem to parallel lions, hyaenas, spotted dogs and Komodo dragons in that
16 they cannot consume their large prey items at a single feasting and often gather in groups at a
17 kill. Conspecifics are attracted from a distance and tough-skinned carcasses need time to putrefy
18 so that the crocodiles can puncture the hide (Pooley 1989). Thus, crocodiles appear likely hosts
19 for kleptoparasitism. However, there are no recorded instances of aggressive kleptoparasitism in
20 this group, either inter- or intraspecific. Crocodilian jaws have no sideways movement or
21 chewing action, so the food must be gulped whole and crocs often work together to tear apart
22 large prey items (Pooley 1989). While all crocodiles other than the one who made the kill are
23 technically partaking of another's meal, cooperative feeding (some crocs hold the carcass while

1 others spin to tear off a portion) suggests that the original crocodile may benefit from the actions
2 of others more than the cost of losing some food at a large kill. Therefore, such an interaction is
3 not necessarily kleptoparasitism. Further studies are needed.

4

5 **Obligate versus facultative kleptoparasitism**

6 All of the kleptoparasites described above are facultative kleptoparasites; they have an
7 alternate, independent feeding mode. Facultative kleptoparasitism is more common than obligate
8 kleptoparasitism. Even sea birds, with the highest number of documented kleptoparasites,
9 contain no known obligate kleptoparasites (Furness 1987). Many kleptoparasitic birds steal food
10 from other birds only during the nesting season, when the hosts aggregate and bring large
11 quantities of food to an identifiable place (Furness 1987). Perhaps this is the most reliable way
12 the kleptoparasites can easily find prospective hosts. Some avian facultative kleptoparasites
13 (frigatebirds, skuas, gulls) obtain a large portion of their diet from kleptoparasitism (Brockmann
14 & Barnard 1979, Hockey & Steele 1990), but only the Arctic skua may contain individuals that
15 subsist throughout the year by kleptoparasitism (Furness 1987).

16 The few known obligate kleptoparasites are mostly restricted to the phylum Arthropoda.
17 Despite an entire genus of spiders (*Argyrodes*) with morphological adaptations for
18 kleptoparasitism (Tso & Severinghaus 1998), only one spider (*Curimagua bayano*) has so far
19 been identified as an obligate kleptoparasite (Vollrath 1978). This species relies on its host to
20 capture and even predigest the prey: the parasite climbs over the host's chelicerae to share the
21 meal (Vollrath 1978). Within the Hymenoptera, "lemon bees" (stingless bees in Central
22 America) have no structures for carrying pollen and pillage other bees' nests, stealing pollen and
23 honey to survive (Wille 1983). In some slave-making ant species, the masters are incapable of

1 feeding themselves and so would go extinct without slaves. *Leptothorax emersoni* ants die when
2 there are no slaves to regurgitate food (Caullery 1952). The Amazonian ant *Polyergus rufescens*
3 has no masticating edges on its mandibles and so relies on *Formica fusca* and *F. rufibarbs* slave
4 ants, acquired as pupae, to establish a nest and feed their masters (Caullery 1952, Read 1970).
5 To establish a new colony, an *Epimyrma stumperi* female invades the nest of *Leptothorax*
6 *nigriceps* ants, masks her scent with host cutaneous secretions, kills the host queen and becomes
7 the new queen (Caullery 1952). The *L. nigriceps* workers then tend *E. stumperi* eggs and larvae,
8 even regurgitating food for workers of the other species (Caullery 1952).

9 Pea crabs (Pinnotheridae), which feed on the food-laden mucus of their host, usually a
10 bivalve, are perhaps the most well-known marine kleptoparasites. Post-sexual maturity, female
11 pea crabs are too large to leave the host (Street 1974, Misra & Ghatak 1983) and so are obligate
12 kleptoparasites. However, the crabs sometimes inadvertently cause gill and mantle damage in the
13 host (Dales 1966, Anderson 1975, Misra & Ghatak 1983, Bierbaum & Ferson 1986),
14 disqualifying the interaction from kleptoparasitism because the host experiences damage beyond
15 mere food loss.

16 A few phyla besides Arthropoda possess obligate kleptoparasites. If a sabellid worm is
17 removed from its tube, any associated hydroid colonies in the genus *Proboscidactyla* (phylum
18 Cnidaria) disappear (Strickland 1971). At least one rhynchocoelan (*Malacobdella grossa*;
19 phylum Nemertea) takes food from the feeding currents of its host (the bivalve *Zirfaea cripata*)
20 and is apparently an obligate kleptoparasite (Gibson & Jennings 1969). Among marine snails,
21 only one species has been identified as potentially an obligate kleptoparasite (Hayami & Kanie
22 1980), and this is a fossil species, so the feeding mode cannot be experimentally verified. In

1 each of the three previous cases, no one has yet investigated whether there is a measurable cost
2 to the host.

3 The rarity of obligate kleptoparasites, in both highly mobile and sedentary associations, is
4 likely the result of a reduction in feeding opportunities: obligates are restricted to subverting
5 food obtained by the host, while facultative kleptoparasites can exploit that source plus any non-
6 harvested food they can subdue or gather. Numerous authors have hypothesized that
7 kleptoparasitism is a frequency-dependent evolutionarily stable strategy, restricting
8 kleptoparasitism to only some members of the population or some times of the year (Brockmann
9 & Barnard 1979, Holmgren 1995).

10 Many kleptoparasites steal food from hosts that feed as the kleptoparasites' ancestors fed
11 (fishing in birds, suspension feeding in snails, capturing prey in webs for spiders), so the addition
12 of kleptoparasitic behaviors may not require adaptations that render the kleptoparasite a poorer
13 independent feeder. Because movement-limited kleptoparasites have a difficult time switching
14 among individual hosts, it is imperative that their hosts obtain enough food to remain viable. In
15 times of food stress, the kleptoparasite may need to feed independently to avoid exerting an
16 excessive, lethal resource drain on the stressed host. The extent to which kleptoparasitism is
17 facultative or obligate falls along a continuum that is determined, in part, by the degree of
18 morphological specialization of the kleptoparasite (especially if that specialization precludes
19 independent feeding) and the level of resistance by the host (discussed in the next section).
20 Comparative studies between kleptoparasitic species and non-kleptoparasitic species within the
21 same taxonomic group are critical to determine the conditions promoting the evolution of
22 kleptoparasitism.

23

1 **Host response: The risk assumed by the kleptoparasite**

2 At first glance, kleptoparasitism appears a relatively cheap and easy way to obtain food.
3 However, its convenience and profitability might lead to selection against its spread through the
4 community, as hosts supporting kleptoparasites suffer decreased fitness (Barnard 1984a). A
5 dichotomy apparently exists in the response of hosts to kleptoparasites: many hosts actively fight
6 against kleptoparasites or attempt to stymie kleptoparasitic activity, but other hosts are either
7 oblivious to the presence of the kleptoparasite or choose to relinquish food without a struggle.
8 Some small kleptoparasites fall below the host's sensory or profitability threshold and are
9 ignored (Vollrath 1984). However, if the parasite is large enough to eat the same food as the
10 host, detection may be inevitable. If rapid ingestion is not an individual's strength, the potential
11 host must use one of a wide range of strategies for dealing with kleptoparasites: retaliation,
12 toleration, compensation and evasion (Barnard 1984a).

13 Hosts may actively fight back to thwart kleptoparasites (*retaliation*). Some
14 kleptoparasites face considerable potential danger because the host can injure or even kill them.
15 Examples include birds that steal from larger predatory birds (Meinertzhagen 1959), whelks that
16 steal from sea stars (Rochette et al. 1995), and scorpionflies that feed while sitting on a spider's
17 web (Vollrath 1984). Many spiders that steal from larger spiders risk becoming a meal for their
18 hosts (Whitehouse 1997).

19 Kleptoparasitism may have driven the evolution of cooperation in some hosts. Biparental
20 cooperation may have evolved in burying beetles (*Nicrophorus* sp.) to protect the carcass against
21 carrion flies (Trumbo 1994). Large African carnivores, such as lions, may increase the size of
22 hunting packs to reduce prey loss to kleptoparasites such as spotted hyenas (Caraco & Wolf
23 1975, Carbone et al. 1997). Turning the tables, hyenas in large numbers fight kleptoparasitic

1 lions (Barnard 1984a). These alterations in the social behavior of the hosts may increase the risk
2 of injury for the thieves.

3 In contrast, some hosts do not pose any threat to kleptoparasites and appear to have no
4 defense against kleptoparasitic activities (*toleration*). A sea otter female does not retaliate after a
5 conspecific holds her pup hostage for food, and tube worms infected by the snail *Trichotropis*
6 *cancellata* display no obvious reaction to this kleptoparasite, even when the snail probes the
7 host's feeding tentacles and mouth or sweeps its shell through the worm's tentacles (Iyengar
8 pers. obs.). Similarly, worker ants are apparently oblivious to the presence of kleptoparasitic fly
9 larvae (*Metopina pachycondylae*) that curl around the anterior end of ant larvae and steal food as
10 the workers feed the larvae (Wheeler 1901, Read 1970). Some hermit crabs host worms (phylum
11 Annelida) that reside in the terminal shell whorls and seize food when the crab eats (Caullery
12 1952). Even though the worm is in close proximity to the crab's mouth when stealing food and
13 lives entirely at the host's expense, the crab makes no attempt to attack the worm (Caullery
14 1952). Some spider hosts merely abandon webs that are heavily infested by kleptoparasites
15 rather than seek and attack the invaders (Vollrath 1984).

16 A host's lack of response to kleptoparasitism does not imply necessarily that the host is not
17 incurring a cost. Certain hosts may be incapable of launching an effective defense (wild dogs
18 are rarely successful in dispelling kleptoparasitic hyenas; Curio 1976, Creel & Creel 1996,
19 Carbone et al. 1997, Gorman et al. 1998), and so the hosts may conserve energy by not reacting.
20 Even if an effective defense is possible, the host will not always react because defense may be
21 uneconomical (Amat & Soriguer 1984). If kleptoparasitism is rare or if the lost prey is relatively
22 unprofitable to recover, retaliation may cost more than tolerance. Barnard (1984a) hypothesized
23 that cheetahs readily abandon kills to kleptoparasites because the costs of defense are greater

1 than the costs of capturing more prey. However, Durant (2000) suggests that the small size of
2 these cats results in an inability to defend their prey from bigger predators. Whether cheetahs
3 have evolved a successful strategy (that of no defense), or barely eke out a living in the face of
4 pressures from larger-bodied kleptoparasites, should be of immense interest to scientists studying
5 potential host responses and the conservation of these cats.

6 Rather than defending prey or tolerating prey loss, a host may compensate for lost prey
7 by feeding longer (*compensation*). This time budget adjustment may detract from other
8 activities, e.g. reproduction. Moreover, for animals already operating near their physiological
9 limits, e.g. wild dogs (Gorman et al. 1998), feeding longer may not be an option. Instead, some
10 hosts attempt to evade kleptoparasites (*evasion*). But fleeing from kleptoparasites can be
11 metabolically expensive, as demonstrated in lapwings, leopards, and puffins (Grant 1971, Curio
12 1976, Barnard 1984a, Furness 1987). Alternative strategies of evasion have evolved, including
13 varying life histories. For example, gall-inducing thrips have evolved either long-lived galls
14 with soldier morphs, short-lived galls with early emergence, or long-lived galls on a tree species
15 rarely attacked by other thrips (Crespi & Abbot 1999), thereby altering their method of resource
16 acquisition. Spiders may shorten the time involved in prey capture or rotate prey items to
17 dislodge feeding kleptoparasites (Vollrath 1984), while birds feed at night, underwater, or in
18 dense flocks to foil kleptoparasites (De Leeuw & Renema 1997). Wild dogs, lapwings (birds),
19 golden plovers (birds), and northern pike (fish), switch to smaller prey that can be consumed
20 rapidly when kleptoparasites are present (Barnard 1984a, Lucas 1987, Carbone et al. 1997,
21 Nilsson & Bronmark 1999). To avoid harassment, lapwings and golden plovers may actually
22 discard large worms rather than consume them if kleptoparasitic gulls are nearby (Barnard

1 1984a). No similar examples of evasion, through any method other than by fleeing, has yet been
2 demonstrated in aquatic invertebrates.

3 Investigating when hosts evolve defenses against kleptoparasitism as opposed to opting
4 for tolerance, compensation or evasion, and the resulting effect these strategies have on the
5 subsequent degree of specialization by the kleptoparasite, should be of immense interest to
6 biologists studying the evolution of biotic interactions.

7

8 **Why is kleptoparasitism often overlooked?**

9 Kleptoparasitic interactions can strongly influence the evolution of the participants.
10 Plagued by kleptoparasites, marine worms grow more slowly (Iyengar 2002a), spiders gain less
11 weight (Grostal & Walter 1997), and some wild dog populations are threatened with extinction
12 (Creel & Creel 1996, Gorman et al. 1998). Hosts develop better "burglar alarms" and thieves rise
13 to the challenge, sometimes leading to co-evolutionary arms races (Dawkins & Krebs 1979).
14 Yet, most evolutionary studies have ignored the selection pressures exerted by kleptoparasitism.
15 Reports of kleptoparasitism are often incidental anecdotes in the midst of studies on other
16 phenomena. Some authors have labeled small animals that steal food as "commensals,"
17 reasoning that a relatively small-sized symbiont would not harm the host (e.g., Sharman 1956,
18 Gotto 1957, Dales 1966, Misra & Ghatak 1983). However, the size of a kleptoparasite is not
19 necessarily correlated with the amount of resources it steals. Ignorance of the impact of
20 kleptoparasitism can skew or invalidate interpretations of other aspects of animal behavior or
21 biology.

22 Adding to the complex nature of kleptoparasitism, some animals shift between trophic
23 strategies, performing kleptoparasitism during some life stages and feeding independently in

1 others, or even switching feeding modes within the same developmental stages. Young
2 harvestfish shelter beneath jellyfish and steal food from the host's tentacles, but gradually begin
3 feeding on the host itself (Mansueti 1963). The aforementioned *Lomechusa strumosa* beetle
4 cohabits with ants and is kleptoparasitic as a larva, but becomes a predator of ant larvae at a later
5 developmental stage (Caullery 1952). In one of the few experimental studies investigating
6 conditions driving different feeding strategies, Koh and Li (2003) found that whether the spider
7 *Argyrodes flavescens* foraged independently or as a kleptoparasite was dependent on the hunger
8 level of the parasite, the type of prey, and the presence of the host. Kleptoparasites' flexible
9 foraging strategies, dependent on their surrounding environmental conditions, make short-term
10 observations under limited conditions result in lower estimates of the frequency and importance
11 of this phenomenon than warranted.

12

13 **Proposed model systems**

14 The model systems for kleptoparasitism to date have largely utilized birds, and most
15 avian studies of kleptoparasites involve interactions between adult birds in flight. These studies
16 are especially limited by large area requirements, the fast movements of the participants and the
17 tendency of birds to form large feeding or nesting groups, all of which lower the ability of the
18 observer to monitor interactions between specific participants. Therefore, I propose that spiders,
19 Hymenoptera and marine snails will prove to be better model systems of kleptoparasitic
20 interactions due to their ease of laboratory and field manipulations, the rate of their interactions,
21 the range of kleptoparasitic behaviors, and the degree of adaptations within closely related
22 groups.

1 Many spiders within the genus *Argyrodes* have specialized in kleptoparasitism, becoming
2 morphologically and behaviorally adapted to this foraging strategy (Tso & Severinghaus 1998).
3 In some cases, kleptoparasitic spiders have evolved specific foraging strategies that allow them
4 to choose among potential hosts, increase their prey capture in the face of competition from other
5 kleptoparasites, and lessen their chance of detection by the host (Vollrath 1979, 1984, Henaut
6 2000). Both the spiders and the Hymenoptera have species that remain in the host's web for
7 their entire lives, providing model systems for kleptoparasites closer to the sedentary end of the
8 spectrum, and other mobile species that move among hosts. In the Hymenoptera, comparisons
9 between genera with and without kleptoparasitic members can shed insight as to the conditions
10 promoting the evolution of kleptoparasitism. Within the superfamily Apoidea (bees),
11 kleptoparasitism has evolved independently at least four times (Iwata 1976). Large trends in
12 kleptoparasitic interactions, such as the correlation between latitude and the frequency of
13 kleptoparasitism in bees, wasps and ants (Wcislo 1981), can lead to predictions of traits
14 important to the evolution of species interactions that can then be examined in other taxonomic
15 groups.

16 Marine kleptoparasites have received much less research attention than terrestrial
17 kleptoparasites, perhaps due to a general ignorance of the diversity of their interactions. Marine
18 snails are perhaps the strongest candidates for new model systems of kleptoparasitism, as they
19 are descended from a wide range of trophic strategies (carnivores, scavengers, parasites and
20 suspension feeders). Most of the documented kleptoparasitic snails are movement-limited
21 individuals from the superfamily Calyptraeacea and at least one species in this group
22 (*Trichotropis cancellata*) has proven hardy and amenable to experimental manipulation.
23 Because snails and their typical hosts move slowly (or not at all) and individuals are relatively

1 easy to mark, field studies can be performed in natural habitats, tracking large numbers of
2 individuals in the wild. Experiments using kleptoparasitic snails can measure actual growth rates
3 and fecundity of the kleptoparasites and their hosts (as in Iyengar 2002a, 2004). Within this one
4 snail superfamily, the numerous kleptoparasites participate in different types of food stealing
5 (some intercept feeding currents, while others reach into the host's mouth), utilize a wide range
6 of hosts, and vary greatly in the importance of kleptoparasitism to their overall caloric intake
7 (Iyengar 2002a, 2002b, 2004). Studies of different populations of the same species, of
8 kleptoparasites descended from scavengers versus suspension feeders, of phylogenetic trends,
9 and comparisons between kleptoparasites and related independent feeders, promise to provide
10 important insight into the field of kleptoparasitism and the evolution of host-parasite
11 interactions.

12

13 **CONCLUSION**

14 Two of the highest priorities of most animals are finding and protecting food (Barnard
15 1984a). Thieves are common, both in the terrestrial and aquatic realms, among invertebrates and
16 vertebrates. Kleptoparasitism is ubiquitous but rarely discussed in sedentary systems. Few
17 studies have quantitatively measured the costs and benefits to both participants in potentially
18 kleptoparasitic interactions, so the true breadth of this behavior is unknown (but see Rochette et
19 al. 1995, Pernet & Kohn 1998, Morissette & Himmelman 2000a, 2000b, Iyengar 2002a, 2004).
20 Investigating the conditions promoting facultative and obligate kleptoparasitism may reveal
21 important insights as to the important selection agents of kleptoparasites. Although modeling
22 kleptoparasitic interactions has received a fair amount of attention (e.g., Hamilton 2002, Broom
23 & Ruxton 2003), few quantitative studies have compared the costs and benefits of

1 kleptoparasitism versus independent foraging (but see Iyengar 2002a, Smith et al. 2002, Koh &
2 Li 2003). The same pair of participants may respond differently in various environments,
3 sometimes resulting in kleptoparasitic interactions, sometimes in mutualistic or commensalistic
4 interactions. Studies examining the costs and benefits to participants in multiple environments
5 and comparing selective pressures across different kleptoparasitic systems are critical to allow
6 meaningful models of the evolution of kleptoparasitism.

7 Kleptoparasitism can affect the morphology and life histories of both the kleptoparasite
8 and the host as selection pressures from the interaction cause evolutionary change. Some of the
9 conditions promoting the evolution of kleptoparasitism as posited by previous avian researchers
10 examining highly mobile participants (Brockmann & Barnard 1979, Paulson 1986) also apply to
11 interactions between sedentary animals: the benefit of additional food must exceed the costs
12 associated with theft, the kleptoparasite is able to learn, there is a reliable cue signaling to the
13 kleptoparasite a host with digestible food that is accessible to the kleptoparasite, and the typical
14 habitat of the host and kleptoparasite are congruent. On the other hand, some requirements vary
15 depending on the level of mobility of the participants and the length of the interaction: short-
16 term interactions can exert a severe negative impact on the host and a high density of hosts with
17 lucrative food items are needed, while long-term associations cannot use a host with a life span
18 shorter than the kleptoparasite's generation time or one that consumes many of the parasite's
19 offspring. As in birds (Barnard 1984a), certain marine and terrestrial invertebrate taxa have a
20 preponderance of kleptoparasitic members: snails in the Capulidae, pea crabs, and certain groups
21 of spiders, bees, ants, beetles, and flies. Additionally, certain host taxa in marine systems have a
22 propensity to harbor kleptoparasites: immobile, suspension-feeding taxa such as bivalves,
23 ascidians, and sedentary worms.

1 Studies of kleptoparasitism can shed light on the evolution of multiple behaviors,
2 particularly shifts between commensalism, parasitism, amensalism, and mutualism. Many
3 milichiid and chloropid flies are kleptoparasites of large spiders (McMillan 1975, Robinson &
4 Robinson 1977, Vollrath 1984, Sivinski et al. 1999), but this behavior has evolved into a
5 cleaning relationship with the spiders for some milichiids (McMillan 1975). How often these
6 shifts happen evolutionarily, under what conditions, and whether they are reversible are some of
7 the major questions studied by evolutionary ecologists. Studies of the potential hosts, preferred
8 hosts, and the reactions of hosts to kleptoparasitism can further our understanding of symbiotic
9 interactions in general.

10

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4

5 * The numbers in square brackets are referred to in Table 1

6

1 Table 1. Taxonomic groups with kleptoparasitic members.
2

Animal Phylum	Group	References‡
Cnidaria	hydroids	1, 15, 19, 80
Platyhelminthes		30, 47
Annelida		15, 19, 23, 26
Arthropoda	flies	56, 66, 68, 75, 76 and references therein, 83, 87, 91
	beetles	15, 49, 83
	bees, wasps and ants	15, 18, 43, 51, 52, 65, 66, 90, 95, 96, 98
	mites and spiders	39, 41, 84, 85, 86, 87, 92, 94
	other insects	2, 24, 48, 93
	caprellids, copepods, and amphipods	7, 19, 32, 81
	crabs	3, 9, 58, 59, 79
Mollusca	slugs	99
	snails	21, 34, 36, 44, 45, 46, 54, 59, 62, 63, 64, 69, 70, 72, 74, 82
Echinodermata	sea stars, brittle stars	16, 40, 59, 60, 77, 78, 88, 97
Chordata	fish	22, 27, 29, 50, 61
	turtles	10, 11, 35, 37, 38, 53
	lizards	4, 33
	birds	6, 12, 18, 28, 57, 71, 73, 89
	mammals	5, 8, 13, 14, 17, 18, 20, 31, 55, 57
	marine mammals	25, 42, 67

3 ‡ Each number can be found in square brackets in the Literature Cited section following the
4 appropriate reference.
5

1 Table 2. Prerequisite conditions for most kleptoparasitic interactions. Adapted from Brockmann
 2 and Barnard (1979).

3

Encourages kleptoparasitism in both mobile and sedentary systems

- 1) Kleptoparasites are opportunistic feeders
 - 2) Food is obtainable and digestible
 - transportation or storage of food by the host
 - kleptoparasite can detect cues from appropriate hosts
 - habitat allows cue transmission
 - 3) Net gain from kleptoparasitism (accounting for elevated risks) is greater than from independent foraging
 - independent feeding is costly*
 - kleptoparasite obtains food without disproportionately increasing its risk of injury
 - kleptoparasite is able to assess the trade-offs of different feeding modes (perhaps via learning)
 - 4) Typical habitat of kleptoparasite and host is congruent
 - (not a necessary requirement if the host is reliably in the same place and the kleptoparasite is highly mobile)
 - 5) Predictable host habits (affiliated with a certain habitat or area)
-

4

5 * Brockman and Barnard (1979)'s requirement that the kleptoparasite experience a food shortage
 6 is incorrect even for avian systems. The present requirement is more accurate. However,
 7 because avian kleptoparasitic interactions often are unsuccessful and involve large energy
 8 expenditures (due to aerial chases), it may be true that the only time kleptoparasitism is more
 9 energetically lucrative than independent feeding is when there is a food shortage for the
 10 kleptoparasite.

11

1 Table 3. Characteristics and requirements that differ between mobile and sedentary
 2 kleptoparasitic interactions.
 3

In mobile systems (acrobatic hosts and kleptoparasites)	In more sedentary systems
1) Interactions are fleeting, the kleptoparasite utilizes many hosts within its lifetime ¹	1) Interactions are long in duration, the kleptoparasite utilizes few hosts within its lifetime (sometimes only one)
2) Extreme negative impact on the host is possible	2) Extreme negative impact on the host is not possible because of limited ability to find a new host if the present one dies
3) Hosts are present in a large concentration ¹	3) One host might be sufficient
4) Hosts must control large quantities of large, high quality food items ¹	4) Individual items do not need to be large, as not much energy is expended by kleptoparasite to steal food and host feeding is continuous. Regular access to adequate food is necessary.
5) Life span of host has no relevance to the time required to sexual maturation in a kleptoparasite	5) Life span of host exceeds a sessile kleptoparasite's time to sexual maturation or hosts aggregate in heterochronous assemblages if kleptoparasite is sedentary.
6) Hosts do not usually interact with the kleptoparasite's offspring, so any life history stipulation is unnecessary	6) Host must not consume a large proportion of the kleptoparasite's offspring, either during larval emergence or settlement

4
 5 ¹ Adapted from Brockmann & Barnard 1979
 6