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KLEPTOPARASITISM IN BIRDS

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Abstract. Kleptoparasitism refers to the interspecific stealing of already procured food, but this paper shows that intraspecific food-stealing is effectively the same behaviour. A comprehensive review of the literature shows that certain orders of birds contain a disproportionate number of kleptoparasitic species. Birds in these orders occupy a limited range of ecological niches and are most commonly either predatory or dietary opportunists. Kleptoparasitism is particularly associated with certain ecological conditions, such as the availability of hosts feeding on large, visible food items and periods of food shortage. Birds show a wide range of socially parasitic feeding interactions of which kleptoparasitism is one extreme. The parasitic pattern of food-stealing is likely to involve frequency-dependent selection and may be an example of an evolutionarily stable strategy.

The term 'clepto-parasitism' or kleptoparasitism was introduced by Rothschild & Clay (1952) to describe the stealing of already procured food by individuals of one species from individuals of another. The same behaviour is also referred to as 'piracy' by many authors (Meinertzhagen 1959, 1964; Ashmole 1971; Nakamura 1972; Hatch 1975; Andersson 1976; Källander 1977) as well as 'food parasitism' (Hopkins & Wiley 1972), 'pilfering' (Rand 1954) and 'robbery' (Hulsman 1976). Although kleptoparasitism is a term that is generally reserved for interspecific stealing of food, the other terms are also used for intraspecific food theft, emphasizing the close relationship between intra- and interspecific feeding patterns. Kleptoparasitic behaviour is known to occur in other animal groups (Wilson 1971), but it appears to be particularly widespread among birds. Species such as frigate-birds (*Fregata* spp.) (Bent 1923; Nelson 1975), skuas (*Stercorarius* spp.) (Meinertzhagen 1959; Grant 1971; Ramsey 1973; Andersson 1976; Furness 1977; Arnason & Grant 1978) and some gulls (*Larus* spp.) (Schmidt 1954; Bergman 1960; Ingolfsson 1969; Hatch 1970; Fuchs 1977; Källander 1977) often procure a significant proportion of their diet through kleptoparasitism. Occasional acts of piracy have been observed in a wide variety of other bird species (see Appendix A).

Most of the recorded instances of kleptoparasitism include only descriptions of the behaviour in a particular species, with little attempt to provide an explanation. Only Rand (1954) has provided any broadly applicable

hypotheses to account for the distribution of kleptoparasitism among birds or to demonstrate its relationship to other forms of intra- and inter-specific feeding. In this paper we review the occurrence of kleptoparasitism among birds and the ecological conditions under which the behaviour emerges. We discuss food stealing as one of a number of feeding interactions. We also discuss the selective pressures acting to maintain kleptoparasitism as a feeding pattern in a population.

Taxonomic Distribution of Kleptoparasitism in Birds

We have reviewed the ornithological literature of the past 40 years, searching for descriptions of behaviour that could be called kleptoparasitic. Although undoubtedly incomplete, this survey is representative of the species which either kleptoparasitize or act as hosts. The survey (Appendices A, B, C) reveals that birds of some orders are more likely to develop kleptoparasitic habits than those of other orders (Table I). For example, only one duck, the American wigeon (*Anas americana*) is a regular kleptoparasite, although ducks are frequently found in mixed-species flocks and are the hosts of other kleptoparasites (Table I). Among such seed- or fruit-eating orders as Galliformes, Columbiformes, and Psittaciformes, kleptoparasitism has never been observed. Among the Falconiformes and Charadriiformes (particularly Stercorariidae and Laridae), many species have been observed kleptoparasitizing other birds. Although the vast majority of bird species are in the order Passeriformes, the incidence of kleptoparasitism between passerines and other birds is infrequent and sporadic. However, passerines are known to steal from

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Table I. The Occurrence of Kleptoparasitism between Birds

Taxon	No. species in taxon	No. kleptoparasitic species in taxon	No. species acting as hosts in taxon	No. species kleptoparasitizing these hosts
Sphenisciformes				
Spheniscidae	18	0	3	6
Struthioniformes	1	0	0	0
Rheiformes	2	0	0	0
Casuariiformes	4	0	0	0
Apterygiformes	3	0	0	0
Tinamiformes	45	0	0	0
Gaviiformes				
Gaviidae	4	0	3	4
Podicipediformes				
Podicipedidae	19	0	3	5
Procellariiformes	99	1	7	12
Diomedidae	13	0	1	1
Procellariidae	61	1	5	10
Hydrobatidae	20	0	1	1
Pelecanoididae	5	0	0	0
Pelecaniformes	58	8	10	23
Phaethontidae	3	0	1	1
Pelecanidae	8	1	1	7
Sulidae	9	2	4	6
Phalacrocoracidae	29	0	3	8
Anhingidae	4	0	0	0
Fregatidae	5	5	1	1
Ciconiiformes	123	7	8	20
Ardeidae	67	4	5	14
Cochleariidae	1	0	0	0
Balaenicipitidae	1	0	0	0
Scopidae	1	0	0	0
Ciconiidae	18	2	2	2
Threskiornithidae	30	1	1	4
Phoenicopteridae	5	0	0	0
Anseriformes	160	3	17	47
Anhimidae	3	0	0	0
Anatidae	157	3	17	47
Falconiformes	298	31	26	60
Cathartidae	7	1	1	1
Sagittariidae	1	0	1	2
Accipitridae	226	22	19	36
Pandionidae	1	0	1	5
Falconidae	63	8	4	16
Galliformes	270	0	0	0
Gruiformes	201	1	4	8
Turnicidae	16	0	0	0
Gruidae	15	0	0	0
Rallidae	130	1	3	7
Otidae	25	0	1	1
(other families)	15	0	0	0
Charadriiformes	325	32	47	132
Jacanidae	8	0	0	0
Rostratulidae	2	0	0	0
Haematopodidae	7	0	1	3

Table I continued

Taxon	No. species in taxon	No. klepto- parasitic species in taxon	No. species acting as hosts in taxon	No. species kleptopara- sitizing these hosts
Charadriidae	70	1	3	7
Scolopacidae	76	0	3	4
Recurvirostridae	9	0	0	0
Phalaropodidae	3	0	0	0
Dromadidae	1	0	0	0
Burhinidae	8	0	0	0
Glareolidae	17	0	0	0
Thinocoridae	4	0	0	0
Chionididae	2	2	0	0
Stercorariidae	5	5	1	1
Laridae	88	23	32	91
Rynchopidae	3	0	1	1
Alcidae	22	1	6	25
Columbiformes	313	0	0	0
Psittaciformes	327	0	0	0
Musophagiformes	23	0	0	0
Cuculiformes	132	0	0	0
Strigiformes	134	2	3	5
Tytonidae	9	0	1	1
Strigidae	125	2	2	4
Caprimulgiformes	98	0	0	0
Apodiformes	385	0	0	0
Coliiformes	6	0	0	0
Trogoniformes	36	0	0	0
Coraciiformes	205	2	2	2
Alcedinidae	91	1	0	0
Todidae	5	0	0	0
Momotidae	8	0	0	0
Meropidae	25	1	0	0
Coraciidae	16	0	1	1
Leptosomatidae	1	0	0	0
Upupidae	2	0	0	0
Phoeniculidae	7	0	0	0
Bucerotidae	50	0	1	1
Piciformes	397	0	0	0
Passeriformes*	5266	23	23	42
Alaudidae	78	0	1	1
Corvidae	110	8	4	6
Paridae	62	2	1	1
Sittidae	22	0	1	2
Cinclidae	5	0	1	1
Troglodytidae	67	0	1	1
Mimidae	35	1	1	1
Turdidae	312	3	7	19
Motacillidae	54	0	1	1
Laniidae	79	4	2	2
Sturnidae	109	1	1	3
Icteridae	94	1	0	0
Ploceidae	301	1	1	2
Fringillidae	459	2	1	2

*Only the families in which kleptoparasitism occurs are included.

insects and spiders' webs more frequently than are other species (Appendix C). The frequency of kleptoparasitism within an order does not appear to be simply a function of the number of species. Rather there appear to be common features between orders which make them more prone to develop kleptoparasitism. It is easy to see, for example, that kleptoparasitism is more common among predatory species such as raptors and gulls than among non-predatory species. What then are the patterns to the incidence of kleptoparasitism?

Interspecific Associations that May Lead to Kleptoparasitism

Association between two species is obviously a prerequisite for the development of kleptoparasitic behaviour. Interspecific associations occur: (1) where predators pursue prey, (2) where the members of one species mob a predatory animal, (3) where individuals forage in mixed-species flocks, (4) where individuals nest in mixed-species aggregations such as seabird colonies, (5) where animals join others in specialized feeding associations such as where one species acts as a 'beater' for another (Rand 1954) and (6) where members of one species feed on the products, scraps or parasites of another (Rand 1954).

1. Association Based on Predation

Many kleptoparasitic species also prey on their host or its young (Meinertzhagen 1959). For example, hawks and eagles prey on ducks and herons, skuas and large gulls kill grebes, auks and passerines, and shrikes hunt passerines (Appendix A). The victim is usually pursued and may well give up its food to the predatory bird as a form of anti-predator behaviour (Meinertzhagen 1941; Grant 1971). This behaviour can then be exploited by the predator as an easy route to already procured food. For example, Temple (1969) observed a turkey vulture (*Cathartes aura*) preying on live great blue heron chicks (*Ardea herodias*) which it took directly from nests. As the chicks grew, however, they were able to defend themselves by pecking the vulture or disgorging food which the vulture then ate or fed to its young. Puffins (*Fratercula arctica*) attempt to escape harassment from gulls and skuas by diving toward the ocean. If they cannot escape, they drop their food which diverts their pursuer (Grant 1971). There are also examples of predatory birds such as kites, accipiters, eagles, falcons and owls satelining prey both from one another (Appendix

A) and from mammals (Appendix B). This behaviour usually involves chasing or directly snatching the prey from the other predator.

2. Association Based on Mobbing

When birds mob a predator, it may be carrying or feeding on a prey item. If the mobbing is successful and the predator driven away, food may be left behind which the birds can then eat. Such appears to be the probable origin of magpies (*Pica pica*) stealing prey from a golden eagle (*Aquila chrysaetos*) (Dixon 1933) and of crows (*Corvus* spp.) stealing from marsh hawks (*Circus cyaneus*), falcons (*Falco* spp.) and kites (*Milvus migrans* and *Haliastur sphenurus*) (Bent 1937; Tinning & Tinning 1970; Balfour 1973; Goodwin 1976).

3. Association Based on Mixed-Species Flocks

Kleptoparasitism is common among species which occur in mixed flocks (Rand 1954). Birds in these groups aggregate because of a common attraction to a rich food source or because they share the same habitat (Rand 1954; Friedmann 1967). In winter, migrant sandpipers, herons and ducks feed together along shorelines and on mudflats (Williams 1953; Meyerrieks & Nellis 1967; Recher & Recher 1969; Rees 1969; Goss-Custard 1970; Haverschmidt 1970; Siegfried & Batt 1972; Reynolds 1974a; Dawson 1975; Raffaele 1975); blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos*) and mistle thrushes (*Turdus viscivorus*) are found on lawns and fields in loose mixed-species flocks (Snow 1958); house sparrows, starlings, pigeons (*Columba* spp.) and chaffinches (*Fringilla coelebs*) aggregate in city parks and gardens, on lawns and in farmyards; and various species of tits (*Parus* spp.) travel in loose mixed-species flocks, aggregating around feeding tables. In these flocks individuals frequently supplant or chase one another and show both inter- and intraspecific kleptoparasitism (Miller 1885; Snow 1958; Summers-Smith 1963; Bird et al. 1973; Kushlan 1978a, b; Schindler 1978; Barnard personal observation; Karlsson personal observation). Vultures (*Gyps* spp., *Torgos tracheliotus*, *Neophron percnopterus*, *Necrosyrtes monachus*), kites, marabou storks (*Leptoptilus crumeniferus*), magpies and carnivores congregate around a carcass and commonly fight or steal food from one another (Meinertzhagen 1959; Kruuk 1967; Brown & Amadon 1968; Houston 1975; Pomeroy 1975). Large numbers of gulls, fulmars (*Puffinus* spp.), terns (*Sterna* spp.), skuas, pelicans (*Pelecanus* spp.) and gannets

(*Morus bassanus*) follow fishing boats and aggregate around fish houses, and gulls are found in large numbers at refuse tips where intra- and interspecific aggression and stealing of food is common (Bent 1921; Flynn 1957; Meinertzhagen 1959; Boswall 1960, 1977; Nakamura 1972; Verbeek 1977b). Later in this paper we will discuss in more detail the relationship between intra- and interspecific food stealing.

4. Association Based on Mixed-Species Nesting Colonies

Kleptoparasitism occurs most frequently among colonial seabirds which are crowded together on small nesting islands (Rand 1954). Here, birds steal food from conspecifics as well as from other species which nest nearby. Adult common terns (*Sterna hirundo*) steal both from other adults and from chicks as they are being fed (Ansingh et al. 1960; Hays 1970). In mixed colonies of terns, the birds begin stealing from each other early in the season when they are carrying fish for mating displays. The attacks continue while they are feeding the chicks (Hopkins & Wiley 1972; Dunn 1973; Fuchs 1977). Gulls also nest in tern colonies, and they steal food from one another as well as from terns (Tinbergen 1932; Ammermann 1958; Goethe 1960; Hatch 1970, 1975; Veen 1977). In colonies of puffins and black guillemots (*Cephus grylle*), jackdaws (*Corvus monedula*) and gulls patrol the ground (Mylne 1960; Birkhead 1974) while skuas fly overhead, attacking the auks as they fly to their burrows (Grant 1971; Arnason & Grant 1978).

5. Association Based on 'Beating'

Many birds take advantage of the feeding activities of other animals which frighten prey or dislodge food, called 'beating' by Rand (1954). Such feeding associations may, in some cases, lead to kleptoparasitism. Antbirds (*Gymnophithys* spp.; *Alethe* spp.) normally follow army or driver ants, feeding on arthropods frightened out of hiding by the ant swarm, but some individuals may occasionally eat the ants or snatch prey directly from their mandibles (Chapin 1939; Rothschild & Clay 1952; Willis 1967, 1968). Similarly, merlins (*Falco columbarius*) may use the hunting activities of other raptors by capturing prey frightened out of hiding (Watson 1977) or by stealing their already procured prey (Meinertzhagen 1959). The carmine bee-eater (*Merops nubicus*) rides on the

backs of large birds such as bustards (*Ardeotis* spp.), storks (*Ciconia* spp.), ostriches (*Struthio camelus*) and secretary birds (*Sagittarius serpentarius*) as well as on large mammals, flying out to catch insects disturbed by its host (North 1944; Jackson 1945; Mackworth-Praed 1946; Grimwood 1964; Boswall 1970; Cunningham-van Someron 1970). Although the bee-eater associations are generally thought to be mutualistic, Moncur (1946) observed a bee-eater taking a large insect from a bustard's bill. Flocks of water birds such as grebes (*Podiceps* spp.), mergansers (*Mergus* spp.), cormorants and pelicans sometimes feed by encircling a school of fish and driving it toward the shore. Egrets and herons run along the shore line spearing fish frightened into the shallows by the flocks (Christman 1957; Parks & Bressler 1963; Emlen & Ambrose 1970; Leck 1971; Fraser 1974) and terns and gulls hover overhead, diving to catch the cornered fish or occasionally to steal an already captured one (Bartholomew 1942; Cottam et al. 1942; Duchrow 1958; Vinicombe 1976). Gulls and terns follow many other species as they feed, including waders (Marshall 1961b; Courser & Dinsmore 1975; Bertin 1977), ducks and mergansers (Ingram 1944; Tebbutt 1961; Gatenby 1968; Gerrard 1975), loons (*Gavia* spp.) and grebes (Pearse 1950; Lehmann 1978), and auks (Alcidae) (Madge 1965; Scott 1972; Cantelo & Gregory 1975; Jones 1975). They sometimes capture aquatic organisms frightened to the surface by the birds' feeding activities, but they also take food by kleptoparasitism (Appendix A).

6. Association Based on Scavenging

Many species of birds act as scavengers on the scraps, faeces or parasites or feed on the wounds of other animals (Bent 1946; Rothschild & Clay 1952; Rand 1954; Bowman & Billeb 1965; Amadon 1967; Haverschmidt 1970; McFarland 1974; Goodwin 1976). In penguin colonies sheathbills (*Chionis* spp.) feed on faeces and dropped food, but they also frequently interfere directly with parental feeding. When a penguin is regurgitating food to its chick, the sheathbill frightens the young bird and grabs its food (Hall 1900; Jones 1963; Watson 1975). Many birds ride on or follow large mammals, crocodiles or predatory fish, feeding on the animal's faeces and parasites or picking up dropped fragments of food (Moreau 1933; Ryder 1957; Attwell 1966a, b; Benson 1964; Thomson 1964; Friedmann 1967; Pooley 1967; Olivier & Laurie

1974). Such behaviour may occasionally lead to birds actually stealing from the host as it manipulates its food (Murphy 1936; Cowan 1968). Early in the breeding season, gulls feed on fish dropped by terns, but as the season progresses, this behaviour develops into direct stealing (Hatch 1970). House sparrows follow American robins, picking up dropped fragments of worms (Kalmbach 1940) or snatching worms directly from the robin's bill (Miller 1885; Pershing 1930). Hummingbirds (Trochilidae) use spiders' webs in constructing a nest. Collecting webs for nests may have led to the habit of stealing the entangled prey (Wolf 1970; Young 1971; Burt et al. 1976; Douglass 1977; Waide & Hailman 1977). In puffin and guillemot colonies, jackdaws, crows and ravens feed on fish fragments dropped near nests, or eat eggs broken by gulls, but in some areas the corvids regularly attack and steal fish directly from the auks (Mylne 1960; Birkhead 1973, 1974; Richford 1978). Gulls and corvids often parasitize the kleptoparasite by following skuas and large gulls as they chase puffins, out-maneuvring them for the dropped food or picking up scraps from the ground (Meinertzhagen 1941; Belopolskii 1961; Grant 1971; Birkhead 1974; Arnason & Grant 1978). Many species feed on scraps at the kill of a carnivore (Bent 1946; Young 1963; Kruuk 1967; Pomeroy 1975) and some may even follow the predator on the hunt (Bent 1946). Marabou storks depend on vultures to loosen meat from carcasses. The storks either pick up scraps dropped by the vultures, threaten the vultures with their long bills and chase them from the food, or they steal outright from them (Houston 1972, 1975). American wigeons regularly steal aquatic vegetation from diving ducks (*Aythya* spp.), coots, swans, geese (*Anser* spp.) and even muskrats (Rodentia, Cricetidae) (Bent 1923; Forbush 1925; Munro 1949; Wick & Penttilla 1957; Fisher 1975; Johnsgard 1975), but they also simply feed on vegetation loosened by the activities of these hosts (Bent 1923; Munro 1949; Anderson 1974; Bailey & Batt 1974). Rothschild & Clay (1952) suggest that the unusual parasitic behaviour of this duck may have evolved from such non-parasitic feeding associations. Although there are many references to feeding associations between grebes and ducks, coots or herons, these do not apparently lead to kleptoparasitism since the grebes are feeding on a different kind of food from their associate (Ashmole et al. 1956; Hobbs 1958; King 1963; Paulson 1969; Siegfried

1971; Mueller et al. 1972; Robson 1975; Burger & Berruti 1977).

It is clear that wherever there are associations between species, kleptoparasitism may occur. It is equally obvious, however, that kleptoparasitism does not always occur when two species are found together. What kinds of ecological or behavioural conditions make kleptoparasitism particularly likely?

Ecological Conditions Facilitating the Evolution of Kleptoparasitism

1. Large Concentrations of Hosts

For kleptoparasitism to become more than of incidental occurrence, there must be large numbers of available hosts. Such is obviously the case in the large seabird colonies where there are hundreds of auks, gulls, terns and skuas nesting in one restricted locality (Dunn 1973; Veen 1977). Gulls steal from lapwings (*Vanellus vanellus*), eiders (*Somateria mollissima*), and cormorants and wigeons steal from diving ducks only where they are found in large flocks (Bartholomew 1942; Munro 1949; Schmidt 1954; Ingolfsson 1969; Källander 1977; Veen 1977). Sparrows kleptoparasitize digger wasps only where there are large numbers of the insects nesting in one area year after year (Ristich 1953; Brockmann, in press).

2. Large Quantities of Food

Systematic kleptoparasitism by skuas, gulls and terns in seabird colonies occurs only during the nesting season when hosts are returning to their territories with large quantities of food for their offspring or mate (Dunn 1973). The kleptoparasitic tern or jackdaw patrols only at times of the day when the maximum number of hosts are arriving at the nesting area (Hatch 1970; Corkhill 1973; Dunn 1973; Birkhead 1974). When gannets, pelicans, boobies and other birds return to their nests, their crops are filled with large stores of food for the young. A puffin may carry up to 28 sand eels in its beak at one time, making it particularly vulnerable to attack (Lockley 1953). Skuas and frigatebirds apparently judge how much food a booby, tern or auk is carrying, only attacking those with filled crops or beaks (Gibson-Hill 1948; Schmidt 1954; Grant 1971).

3. Large, High-quality Food Items

A tern carrying a large piece of food is more subject to attack from a marauding tern or gull than a bird carrying a small food item (Hopkins & Wiley 1972; Dunn 1973; Fuchs 1977; Veen

1977). However, terns with larger prey may be more vigilant, because attacks on such individuals are not necessarily more successful (Dunn 1973; Fuchs 1977). Only when hosts such as lapwings, thrushes, herons, ducks or swans are feeding on large, energy-rich sources of food such as worms, fish, or edible mussels are they attacked by gulls, herons, thrushes or sparrows (Evans 1908; Pershing 1930; van Tyne 1946; Brian & Brian 1947; Steiniger 1952; Snow 1958; Bergman 1960; Ingolfsson 1969; Bird et al. 1973; Payne & Howe 1976; Källander 1977; Kushlan 1978a, b). In fact, birds only rarely steal plant food from one another (except wigeons and coots, see Appendix A) and when they do, it is often because normal sources of food are not available (Söding 1949; Sage 1963; Siegfried 1972). For example, gulls can apparently tell whether a swan is feeding on vegetation or mussels and attacks only when the swan is bringing a mussel to the surface (Källander 1975). The lower food value of vegetation may make stealing plant material not worth the effort.

4. Food Supply Predictable

If the habits of the host are predictable, then kleptoparasitism is more likely to develop. Puffins repeatedly return to the same burrow with large quantities of fish for their offspring and parent terns return to the same location in the colony to feed their young. Gulls, skuas, terns, and jackdaws simply patrol specific areas in the colony for incoming hosts (Duchrow 1958; Grant 1971) or wait in the grass near the nest (Birkhead 1974).

5. Food Visible

One of the factors that may make kleptoparasitism an expensive strategy is the amount of time and energy invested in chasing hosts without food. Where food is conspicuously carried in the beak or talons as in puffins, terns and raptors, kleptoparasitism is more likely (Zusi 1958; Grant 1971). Only individuals with visible food in the bill are attacked or pursued by a kleptoparasite (Palmer 1941; Brian & Brian 1947; Snow 1958; Zusi 1958; Goethe 1960; Stichmann 1965; Bengtson 1966; Nakamura 1972; Siegfried 1972; Dunn 1973; Fuchs 1977). Aquatic species such as mergansers and eiders which must surface to eat their food (Harrison & Harrison 1962) are more vulnerable than those which capture and swallow their food below the surface such as grebes (Vinicombe 1976). When an individual must manipulate an unusually large prey item

at the surface, kleptoparasitism is more likely to occur (Bengtson 1966; Grubb 1971; Reynolds 1977; Kushlan 1978). Birds, such as terns, that present fish during courtship displays are particularly subject to attack (Dunn 1973; Birkhead 1974; Fuchs 1977). Certainly sparrows spend little or no time chasing digger wasps which are not carrying large and conspicuous katydid prey (Brockmann, in press).

6. Food Shortage

Several authors mention that kleptoparasitism by frigatebirds, gulls and terns occurs more frequently during years of a food shortage or during the winter months (Munro 1949; Palmer 1941; Snow 1958; Bergman 1960; King 1966; Hays 1970). Kleptoparasitism is also more common when weather or other physical conditions such as tidal cycles preclude the parasite feeding on its own (Rooth 1958; Zusi 1958; Bengtson 1966; Ingolfsson 1969; Veen 1977). When parasites are feeding chicks and both food and time are at a premium, kleptoparasitism is more common (Rooth 1958; Grant 1971; Hatch 1975). In flocks of antbirds, there is a strict dominance order, with some individuals having primary access to the insects flushed by the army ant swarm. Subordinate individuals presumably do not have as much food available to them and they are the only birds observed actually stealing prey from the ants (Willis 1967, 1968). In a captive group of house sparrows feeding on dispersed seed, the most persistent initiator of interactions was a bird who was lowest in rank in a previously determined dominance order (Barnard 1978). Similarly feeding associations without kleptoparasitism (Bailey & Batt 1974) as well as intraspecific aggression are more frequent when food is scarce (Lockie 1956; Recher & Recher 1969; Goss-Custard 1970).

Behaviour that Facilitates the Evolution of Kleptoparasitism

1. Behaviour of Parasite

Many kleptoparasitic species are opportunists, taking advantage of any small supply of food they can find (Rand 1954). Blackbirds, house sparrows, starlings, shrikes (*Lanius* spp.), and jackdaws are extremely versatile feeders, exploiting a wide variety of ephemeral food supplies (Richardson 1938; Kalmbach 1940; Snow 1958; Caldwell 1966; Birkhead 1974). Kleptoparasitism is only one of a wide range of opportunistic feeding patterns shown by these species.

A particularly good example of a bird developing kleptoparasitism opportunistically is given by Bengtson (1966). He observed a group of horned grebes (*Podiceps auritus*) feeding on an Icelandic lake. Arctic terns (*Sterna paradisaea*) were diving among the grebes. When a surfacing grebe dropped a fish, a tern which was flying overhead, immediately plunged to the surface and retrieved the fish. The next time the grebe brought a fish to the surface, the tern swooped down on it, causing it to dive below the surface and drop its fish. Bengtson had never before seen kleptoparasitic behaviour at this locality and suggested that it may originate by just such accidents.

Acts of kleptoparasitism often involve feats of considerable aerobic skill (Belopolskii 1961; Bengtson 1966; Hopkins & Wiley 1972; Nakamura 1972; Furness 1977; Källander personal communication). Skuas have been observed flying directly toward puffins, turning over in flight and snatching fish directly from the bill of a flying bird (Andersson 1976). Similarly, kestrels have been observed rolling over in flight, snatching a small mammal from a flying barn owl (*Tyto alba*) (Everett 1968). Snowy and short-eared owls (*Asio flammeus*) steal in a similar manner from marsh hawks and kestrels (Reese 1973; Bildstein & Ashby 1975; Duffy et al. 1976). Such agility may facilitate the emergence of kleptoparasitism as a persistent pattern between some species.

2. Behaviour and Habitat of Host

Some hosts such as swans, mergansers and shrikes bite at or chase the kleptoparasites or evade their attacks in other ways (Lovell 1945; Whitaker 1955; Nilsson 1965; Källander 1977) whereas thrushes, pelicans, ducks and sandpipers do not defend themselves (Pershing 1930; Baldwin 1946; van Tyne 1946; Brian & Brian 1947; Ingolfsson 1969; Bird et al. 1973; Payne & Howe 1976; Dummigan 1977). For many hosts defence may not be energetically worthwhile (Bird et al. 1973). Gulls and jackdaws increase their effectiveness as parasites by hiding in the grass near puffin or guillemot burrows (Mylne 1960; Birkhead 1974). Puffins escape attacks by either dashing headlong into their burrows or by not landing if a parasite is present. Individuals with nests well inland or on shallower slopes suffer significantly higher parasitism than those with nests nearer the shore or on steeper slopes (Grant 1971; Grant & Nettleship 1971; Nettleship 1972). The habitat as well as the

behaviour of the host may affect its chances of being parasitized.

Chasing and pursuing an animal to steal its food or waiting for an animal to return with food appears to be expensive in terms of energy and time. Such behaviour would only be profitable under some circumstances. When predatory or opportunistic species are found in the same habitat with species which are feeding on large food items, then kleptoparasitism occasionally becomes a profitable way of obtaining food. When there are considerable numbers of hosts, predictably bringing large quantities of food to a fixed location, and particularly when food is scarce, then kleptoparasitism may become an important source of food. This combination of characteristics appears to account for the frequency with which certain species such as gulls, skuas and terns become kleptoparasites as well as the frequency with which others such as pelicans, auks, terns and thrushes become hosts (Table I).

Intra- and Interspecific Kleptoparasitism Form a Continuum with Other Feeding Interactions

When a number of individuals feed within sight of each other, each inadvertently furnishes information about its feeding success which can be used by others. The various advantages that accrue from interacting socially during feeding, point to the ways in which food thievery may emerge both within and between species. We suggest that there is no fundamental distinction between intra- and interspecific kleptoparasitism and that there is a direct analogy between 'parasitic' individuals within a species and parasitic species within mixed groups.

The advantages gained from a particular pattern of individual behaviour leading to interaction depend on the distribution and type of food being exploited. Since most naturally occurring food is both heterogeneous and to some degree clumped (Taylor 1961; Southwood 1966), it is clearly beneficial for an animal to monitor the feeding success of surrounding individuals. In laboratory experiments with small groups of great tits (*Parus major*), Krebs et al. (1972) found that a tit copies the perch position of a bird that has just found a mealworm. Perch-copying behaviour results in each bird achieving a higher capture rate when in a group than when feeding alone. Similar observations of the enhancing effect of intraspecific social learning on feeding efficiency have been made in a number of other species (Swynnerton

1942; Fisher & Hinde 1949; Hinde & Fisher 1951; Lockie 1956; Klopfer 1959; Turner 1961; Goss-Custard 1970; Murton 1971; Patterson 1975). Similarly, when birds associate in mixed-species flocks, social learning not only results in the location of more profitable food sites and the direction of attention to the most abundant food (Rubenstein et al. 1977), but also increases the probability that an individual will exploit a novel type of food or feeding location. Krebs (1973) found that both black-capped chickadees (*Parus atricapillus*) and chestnut-backed chickadees (*P. rufescens*) were more likely to discover a completely new foraging location if they were in the presence of an experienced bird of the other species. Clearly when birds are feeding socially they are observing the feeding behaviour of other individuals in the group and are taking advantage of this information. However, the examples discussed are 'casual' interactions, that is, individuals are simply capitalizing on available feeding information. Considering the many advantages that accrue from feeding interactions, we might expect selection to favour individuals which *specialize* in intra- or inter-specific interactions.

Studies on captive house sparrows by one of us (C.J.B.) show that certain individuals ('copiers') concentrate on interacting (following, copying or snatching food) at the expense of others ('searchers'). In a series of experiments, small groups of house sparrows were allowed to forage for patchily distributed mealworms concealed in wells on a hardboard grid. 'Copiers' not only took a larger proportion of their captures through non-aggressive and aggressive interactions than 'searchers' (58% as compared to 26% for 'searchers') but they also spent much less time searching for food (as defined by characteristic head-cocking and zig-zag hopping). 'Copiers' clearly took advantage of 'searchers' since they made little effort to search for food themselves and depended mainly on the patches of food located by 'searchers' (Krebs & Barnard, in press). Such observations lead naturally to the question of what influences the frequency of searchers and copiers in a population, which we will discuss in the next section.

Although there do not appear to be many other recorded instances of intraspecific parasitism of this kind in birds, such behaviour is a well-known interspecific pattern, as we have shown. For example, Emlen & Ambrose (1970) observed that when snowy egrets used flocks of

red-breasted mergansers to locate and obtain fish, they made no attempt to feed prior to the arrival of the mergansers. Only as the mergansers approached the shore, driving fish in front of them, did the egrets begin feeding. When the mergansers moved away, the egrets followed them, and the process was repeated. As Emlen & Ambrose point out, the behaviour of the egrets surpasses the bounds of casual opportunism.

A more vivid example involves cattle egrets. Individuals of this opportunistic species may feed alone or in flocks (Reynolds 1965). When in flocks they show aggressive interactions (e.g. one bird displacing another) or sometimes leap-frog feeding, i.e. using conspecifics as beaters (Blaker 1969; Wiese & Crawford 1974). Cattle egrets also associate with herds of feeding ungulates which disturb their insect prey (Rice 1963; Skead 1966; Benson & Penny 1971). These associations not only increase their capture rate, but also decrease their energy expenditure (Heatwole 1965; Dinsmore 1973). Where cattle are confined overnight, the egrets do not leave their roosts until the cattle are released in the morning (Rothschild & Clay 1952). Dawn (1959) reported behaviour which takes these associations a stage further. When cattle were resting on the ground, groups of 10 to 20 egrets made repeated, short, circular flights over the herd, bouncing off the ground between the cattle. The beating wings apparently disturbed the cattle, which rose and walked about, disturbing more insects for the egrets. Dawn saw several such incidents which appear to be deliberate attempts by the egrets to change the behaviour of the cattle to obtain food. Bearing in mind the extent to which these birds make use of each other and of other species such as cattle, it is not surprising that, given the opportunity, cattle egrets emerge as classic kleptoparasites (Feare 1975).

It is clear that birds can specialize within a range of socially parasitic behaviour. The precise form of the parasitism, whether using other individuals to locate the food, influencing the behaviour of others so as to increase the amount of food available, or actually stealing food from another individual, depends on the particular feeding opportunities available. Kleptoparasitism is only one form among many socially parasitic feeding interactions which emerge under particular environmental conditions. At present there is no reason to doubt that natural selection acts in essentially the same way whether

the association involves intra- or interspecific interactions, but this matter deserves further study.

Is Kleptoparasitism a Feeding 'Strategy'?

One of the striking features of kleptoparasitism is that the behaviour is far more common in some populations than in others (Rand 1954; Bergman 1960; Nilsson 1965; Stichmann 1965; Burton 1968; Neub 1970). In many species kleptoparasitism is simply the result of a chance encounter by a bird pre-adapted to capitalize on a fortuitous feeding opportunity. But for others, kleptoparasitism is often a way of life. When black-headed and common gulls steal from ducks and lapwings, when jaegers pirate auks, when frigatebirds attack boobies and when sheathbills interfere with penguin chicks, the host may be acquiring a significant proportion of its diet through kleptoparasitism. In addition to the ecological factors we have already discussed, the frequency of regular kleptoparasitic behaviour in a population may be also influenced by intraspecific social factors. Kleptoparasitism may be traditional and spreading regionally through observational learning (Neub 1970; Brockmann, in press). But if kleptoparasitism is a regular feeding strategy, then there will be selection against the behaviour if it is not as successful in terms of long term reproductive success, as other feeding strategies in the population (Kushlan 1978b). Furthermore, and this is an important and often overlooked point, the success of a parasite may depend on the number of other kleptoparasites in the population (Arnason 1978). That is, selection for kleptoparasitism may be frequency-dependent (Dawkins, in press).

As an example, consider a population of Arctic skuas. For the purposes of this explanation let us say that in the population there are two feeding strategies: a parasitic one, where the skua chases puffins and steals fish and a predatory one, where the skua actually hunts birds. If there are too many parasitic skuas, competition among them may become so fierce that selection favours predatory birds, and vice versa. There could be an equilibrium ratio of parasites to hunters such that each of the two strategies does equally well: the evolutionarily stable state or ESS of the population. By equally well we mean that the long term reproductive success or pay-off to each strategy is equal. When the population deviates from the ESS, then there is selection against individuals

using the feeding method which is more frequent than prescribed by the ESS (Maynard Smith & Price 1973; Ayala & Campbell 1974; Maynard Smith 1974; Dawkins 1976; Maynard Smith & Parker 1976). There is not necessarily one best feeding strategy, but there may be evolutionarily stable ones in a population (Dawkins, in press).

Kleptoparasitism may be a pattern adopted by most members of the population at one time or another (Grant 1971; Dunn 1973; Diamond 1975; Hatch 1975; Arnason & Grant 1978) or it may be characteristic of particular individuals (Young 1971; Corkhill 1973; Birkhead 1974; Evans 1975), but in either case selection acts in a similar way according to the ESS model. When the feeding behaviour is characteristic of particular individuals, then the model predicts that there would be selection for a stable ratio of parasites to hunters. When the feeding behaviour is shown by all individuals in the population, then the model predicts that selection would act on the proportion of decisions taken by those individuals, i.e. there would be selection against individuals who chose to parasitize too frequently.

We have suggested that when kleptoparasitism is a persistent and frequent pattern in a population, then it is possible that it may be an evolutionarily stable feeding strategy. However, there are other possible explanations for the presence of several feeding patterns within a population (Dawkins, in press; Brockmann et al., in press). Animals may steal when they are young (Pettitt 1952) or when no other food is available. The behaviour may result from a particular individual making the best of its current unfortunate circumstances. Only quantitative data comparing relative success of different patterns will resolve the question of whether kleptoparasitism is truly an alternative feeding strategy in a population.

In the initial examples, we chose a simple two strategy system: parasite or predator. However, the descriptions of most observers reveal far more complex sets of possible strategies. Källander (1977) surveyed large numbers of feeding black-headed gulls (*Larus ridibundus*) during winter and found that they were either (1) kleptoparasitizing lapwings, (2) feeding on the ground, (3) hunting from the air, or (4) following the plough. He showed that there were advantages to stealing from lapwings over following the plough, but the pay-offs to each strategy were difficult to measure. The frequency

of gulls engaging in these different strategies varied markedly from one census to the next. It is possible that such variation reflects temporal changes in the pay-offs and hence different ESSs. Grant (1971) described seven different feeding strategies of skuas at a seabird colony. Which strategy a skua chose depended on the amount of food involved, the chances of success, the presence of various secondary parasites such as gulls and ravens, and the numbers of other skuas also engaging in the behaviour. If, for example, a skua chose to sit and wait on the ground near puffin burrows, its exact position involved a compromise between an area where the numbers of puffins were high but the numbers of skuas were also high and an area where there were fewer puffins but there were also fewer skuas. Selection should lead to skuas choosing these two localities in the proportions that result in each strategy doing equally well (Fretwell & Lucas 1969; Fretwell 1972).

A parasite may show at least two separate kleptoparasitic strategies: (a) initiate an attack or (b) join an attack already in progress (Hatch 1970, 1975; Verbeek 1977b; Arnason & Grant 1978). As might be expected, the probability of the host losing its prey increases with the numbers of parasites chasing it, but the average yield per parasite decreases with group size. These authors did not measure the relative success of the two strategies. Hatch (1975) showed that when initiators were joined by others, they were less successful than the joiners, but he neglected to show the overall success of the initiator strategy under each condition. It appears that early in the season, when most birds were initiators, joiners did better than initiators (in terms of rate of capture) and vice versa late in the season. Arnason & Grant (1978) mention that although their sample size was small, there appeared to be no significant differences in the relative success of the two strategies. These results are exactly what we would expect if selection is favouring a stable ratio between initiators and joiners.

The hosts could be affected by frequency-dependent selection as well. The probability of a puffin getting to its burrow without being intercepted depends on the height at which it flies, how far inland its nest is and the numbers of both parasites and other puffins present. A lone puffin is an easy target, but one flying with many others can effectively insulate itself from attack (Grant 1971; Nettleship 1972; Arnason & Grant 1978).

It is easy to guess that kleptoparasitism involves frequency-dependent selection, but the details are difficult to measure. Data must include the proportion of different strategies in the population and their relative success at that frequency. Ideally, frequency of a behaviour pattern should be altered experimentally in order to test for the effects of frequency-dependent selection. Whether interest is focussed on the effects of kleptoparasitism on the host population (Tinbergen 1932; Hatch 1970; Nettleship 1972; Birkhead 1974; Fuchs 1977) or on competition between two parasitic species (Hopkins & Wiley 1972; Verbeek 1977a, b) or simply on kleptoparasitism as an intriguing co-evolutionary game, it may be important to consider the effects of frequency-dependent selection.

Conclusions

A review of kleptoparasitism among birds makes it abundantly clear that certain orders contain a disproportionate number of kleptoparasitic species. In particular, the Falconiformes and Charadriiformes include about 60% of the recorded species showing kleptoparasitic behaviour although they include only 7% of the known bird species of the world. Clearly the orders containing kleptoparasites have little in common phylogenetically, so what have they in common that facilitates the development of kleptoparasitism?

The above discussion has pointed to several ecological factors which appear to promote kleptoparasitism. An obvious prerequisite is regular association with other individuals and in particular, regular association on or near the feeding grounds. Such associations may occur through mixed-species breeding colonies (e.g. Stercorariidae, Laridae) or feeding flocks (e.g. Anatidae, Turdidae) or they may be the result of predatory interactions (e.g. Accipitridae, Falconidae, Strigidae). Within these categories there are more fine-grained levels of opportunity which govern the emergence of kleptoparasitic relationships. These are mainly the result of the type and abundance of the 'shared' food supply and the opportunities for profitable interactions.

Clearly, where a species feeds on a range of food items, only some of these present opportunities for food-stealing. Selection acts to maintain a relationship between parasite and host if the advantages to the parasite are great enough. There are several modes of interaction, each profitable in different situations. When

birds are feeding on small, cryptic and clumped prey such as seeds and small invertebrates, area-copying is more profitable than trying to snatch the prey from the finder's bill; for large prey, such as earthworms, the opposite is true. These rules apply equally to interactions among conspecifics and heterospecifics.

For a wide-ranging species, food sources vary considerably from place to place as do the opportunities for interaction. The range of interactions from intraspecific copying to various forms of social parasitism seen in such species as house sparrows and cattle egrets, reflect the varied range of opportunities for interaction. Both species capitalize on local feeding conditions without specializing on any one food type. This capitalization may take the form of copier individuals or of kleptoparasites in single-species flocks.

The ability of the wide-ranging opportunist to become parasitic is just one route through which kleptoparasitism can emerge. Selection may also act on a more specialized species to reduce its spectrum of feeding patterns and interactions to a few highly profitable ones. Large mixed colonies of fishing birds provide the ideal environment for kleptoparasitism with a plentiful supply of food items which are easily stolen. It is in this kind of environment that we find specialized kleptoparasites such as frigatebirds and skuas. Specializations by frigatebirds include small unwebbed feet, a vestigial uropygial gland which greatly reduces the amount of oil in the feathers and a wing span to body weight ratio which is greater than for any other bird species. These adaptations greatly facilitate aerobic flight, but they also mean that the birds can no longer enter the water from which most of their food originates (Nelson 1967).

Another type of feeding opportunity arises as a spin-off from predation, as for example, in the association between some accipiters and their prey. Alternatively, many raptors are kleptoparasitic on each other. As Rudebeck (1950, 1951) pointed out, the hunting success of most raptors is generally extremely low, so an immense advantage can be gained by usurping the already immobile prey of another bird.

Although we have talked mainly in terms of predation leading to kleptoparasitism, it is entirely possible for the reverse process to occur. We have found no documented examples of this, but it is not difficult to envisage how it might happen. In the house sparrow-digger wasp relationship, (Brockmann, in press), the

sparrows probably did not arrive at their kleptoparasitism through predation on the wasps, but they are known to prey on other large and mobile insects (Summers-Smith 1963). In time individuals may arise which extend their use of the wasps to actually feeding on them.

Apart from the element of feeding opportunity, there are further factors which may determine which species become kleptoparasitic. Agility is clearly an asset if an animal is to be repeatedly successful in interactions, particularly where these interactions take place in the air. From this point of view, birds like *Fregatidae* and *Stercorariidae* (and to some extent other *larids* and *corvids*), which are built for sustained and manoeuvrable flight, are at a great initial advantage and this may be a further reason for their predominance as kleptoparasites. M. Andersson (personal communication) suggests that such morphological and behavioural preadaptations are of major importance in the evolution of kleptoparasitism.

There does not appear to be a single clear-cut rule which governs the emergence of kleptoparasitism, rather it arises through a variety of opportunistic channels. A key factor in a species becoming a specialist may be the pay-offs for a kleptoparasitic habit as compared with other feeding strategies. If kleptoparasitism results in obtaining more food at less cost, then there will be rapid selection for the necessary patterns of interaction. However, since selection for kleptoparasitism is likely to be frequency dependent, a stable ratio between parasites and individuals using other feeding strategies may evolve.

Detailed studies of the costs and benefits of kleptoparasitic behaviour with respect to other feeding strategies are badly needed. Such studies will allow us to model and predict the emergence of kleptoparasitism for various species mixtures, in various environments and at different times of the year. They may also allow us to predict the number of parasites in a population. Food-stealing may occur between or within most species, given the kinds of opportunities discussed in this paper, but certain species possess a greater ecological potential to specialize.

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APPENDIX A: A Review of Kleptoparasitism between Birds (based on taxonomic classification of Clements (1974))

Kleptoparasite*	Host*	Behaviour	Pred.†	References‡	
Procellariiformes					
Procellariidae					
Fulmar (<i>Fulmarus glacialis</i>)	Gulls (<i>Larus</i> spp.)	2, d		71, 117	
Pelecaniformes					
Pelecanidae					
Brown Pelican (<i>Pelecanus occidentalis</i>)	Gulls (<i>Larus</i> spp.)	s		168	
Sulidae					
Gannet (<i>Morus bassanus</i>)	Herring gull (<i>Larus argentatus</i>)	2, s		61	
Brown Booby (<i>Sula leucogaster</i>)	Masked Booby (<i>Sula dactylatra</i>)	2, g		172	
	Great Frigatebird (<i>Fregata minor</i>)	d		154	
Fregatidae					
Frigatebirds (<i>Fregata</i> spp.)	Shearwater (<i>Puffinus</i> sp.)	7, d		129	
	Tropicbird (<i>Phaethon</i> sp.)	7, d		21, 129	
	Brown Pelican (<i>Pelecanus occidentalis</i>)	7, d, s		20, 88	
	Red-footed Booby (<i>Sula sula</i>)		6, 7, 8, 9,	×	2, 47, 66, 129,
			16, g		154, 192
	Brown Booby (<i>Sula leucogaster</i>)	7, 8, 9, g	×	20, 88, 126	
	Cormorant (<i>Phalacrocorax</i> sp.)	7, d	×	2, 20	
	Gulls (<i>Larus</i> spp.)	6, 7, d	×	2, 20, 129	
	Laughing Gull (<i>Larus atricilla</i>)	6, d, g	×	19	
	Swallow-tailed Gull (<i>Creagrus furcatus</i>)	2, d		75	
	Terns (<i>Sterna</i> spp.)	6, d	×	2, 20, 129	
	Noddy Tern (<i>Anous stolidus</i>)	6, d, g	×	19	
	Ciconiiformes				
Ardeidae					
Great Blue Heron (<i>Ardea herodias</i>)	Great Egret (<i>Casmerodius albus</i>)	5, 6, d		104	
	White Ibis (<i>Eudocimus albus</i>)	5, 6, d		104	
Gray Heron (<i>Ardea cinerea</i>)	Great Black-backed gull (<i>Larus marinus</i>)	6, 8, d	×	112	
Cattle Egret (<i>Bubulcus ibis</i>)	Sooty Tern (chicks) (<i>Sterna fuscata</i>)	5, 6, g	×	59	
Great Egret (<i>Casmerodius albus</i>)	Little Blue Heron (<i>Florida caerulea</i>)	5, 6, d		104	
	White Ibis (<i>Eudocimus albus</i>)	5, 6, d		104	
Ciconiidae					
Wood Stork (<i>Mycteria americana</i>)	Great Blue Heron (<i>Ardea herodias</i>)	5, 6, d		104	
	Great Egret (<i>Casmerodius albus</i>)	5, 6, d		104	
	Little Blue Heron (<i>Florida caerulea</i>)	5, 6, d		104	
	White Ibis (<i>Eudocimus albus</i>)	5, 6, d		104	
Marabou Stork (<i>Leptoptilos crumeniferus</i>)	African White-backed Vulture (<i>Gyps africanus</i>)	s		86, 87	
Threskiornithidae					
White Ibis (<i>Eudocimus albus</i>)	Little Blue Heron (<i>Florida caerulea</i>)	5, 6, d		104	
Anseriformes					
Anatidae					
European Wigeon (<i>Anas penelope</i>)	European Coot (<i>Fulica atra</i>)	s		176	
	American Wigeon (<i>Anas americana</i>)	Whistling Swan (<i>Cygnus (Olor) columbianus</i>)		92, 125	
	Redhead (<i>Aythya americana</i>)	5, d, s		62, 92, 125	
	Greater Scaup (<i>Aythya marila</i>)	5, d, s		21, 62, 125	
	Canvasback (<i>Aythya valisineria</i>)	5, d, s		21, 62, 92, 125	
	Coot (<i>Fulica americana</i>)	5, d, s		21, 62, 160	
Common Eider (<i>Somateria mollissima</i>)	Common Merganser (Goosander) (<i>Mergus merganser</i>)	5, s		18, 92, 125	

*If Gruson (1976) and Morony et al. (1975) disagree with Clements, a second common, generic or specific name is given in parentheses.

†The kleptoparasite is also a predator on the host or its young.

‡Each number can be found in square brackets in the References following the appropriate reference.

Falconiformes

Cathartidae

Turkey Vulture (*Cathartes aura*) Great Blue Heron (chicks)
(*Ardea herodias*) 8, g 183

Accipitridae

Honey Buzzard (*Pernis apivorus*) Secretary Bird (*Sagittarius serpentarius*) 2, d 117
Peregrine Falcon (*Falco peregrinus*) 6, d 117
Black Kite (*Milvus migrans*) Marabou Stork (*Leptoptilos crumeniferus*) 7, d 145
Eagle (*Haliaeetus* sp.) 6, d 41, 117
Common Buzzard (*Buteo buteo*) 6, d 117
Hooded Vulture (*Neophron monachus*) 7, d 145
Egyptian Vulture (*Neophron percnopterus*) 2, d 117
Peregrine Falcon (*Falco peregrinus*) 2, d 117
Pied Crow (*Corvus albus*) 7, d 145

European Sparrowhawk (*Accipiter nisus*) Honey Buzzard (*Pernis apivorus*) 6, d 117
Common Kestrel (*Falco tinnunculus*) 6, d 174

Savanna Hawk (*Heterospizias meridionalis*) Maguari Stork (*Euxenura maguari*) 6, d 41

Red-tailed Hawk (*Buteo jamaicensis*) Peregrine Falcon (*Falco peregrinus*) 2, d 16

Rough-legged Hawk (*Buteo lagopus*) Marsh Hawk (Hen Harrier) (*Circus cyaneus*) 6, d 41, 100

Tawny Eagle (*Aquila rapax*) Common Buzzard (*Buteo buteo*) 6, d 117
African Fish Eagle (*Haliaeetus vocifer*) 6, d 40
Falcon (*Falco* sp.) 6, d 117

Verreaux's Eagle (*Aquila verreauxii*) Martial Eagle (*Polemaetus bellicosus*) 6, d 41

African Fish Eagle (*Haliaeetus vocifer*) Pelican (*Pelecanus* sp.) 6, d 11, 41, 117, 118, 178
Cormorant (*Phalacrocorax* sp.) 6, d 11
Heron (*Ardea* sp.) 6, d × 41, 117, 118, 178
Kite (*Milvus* sp.) 6, d 41, 178
Osprey (*Pandion haliaetus*) 6, d 40, 41, 117, 118, 178

White-bellied Sea Eagle (*Haliaeetus leucogaster*) Whistling Kite (*Haliastur sphenurus*) 6, d 148
Osprey (*Pandion haliaetus*) 6, d 157

Bald Eagle (*Haliaeetus leucocephalus*) Common Merganser (*Mergus merganser*) 2, d × 73
Vulture (*Cathartes* sp.) 6, g 23, 41, 117
Marsh Hawk (*Circus cyaneus*) 7, d 8
Osprey (*Pandion haliaetus*) 6, d 23, 41, 88

White-tailed Eagle (*Haliaeetus albicilla*) Golden Eagle (*Aquila chrysaetos*) 6, d 143, 158
Osprey (*Pandion haliaetus*) 2, d 97

Sea Eagle (*Haliaeetus* sp.) Kite (*Milvus* sp.) 6, d 41
Osprey (*Pandion haliaetus*) 6, d 41

Lappet-faced Vulture (*Torgos tracheliotus*) White-headed Vulture (*Trionocephs occipitalis*) 5, d 101
Ruppell's Griffon Vulture (*Gyps ruppellii*) 5, d 101, 142

African White-backed Vulture (*Gyps africanus*) 5, d 101

Ruppell's Griffon Vulture (*Gyps ruppellii*) African White-backed Vulture (*Gyps africanus*) 5, d 101

African White-backed Vulture (*Gyps africanus*) Ruppell's Griffon Vulture (*Gyps ruppellii*) 5, d 101

Hooded Vulture (*Necrosyrtes monachus*) Egyptian Vulture (*Neophron percnopterus*) 5, d 101

Marsh Hawk (Hen Harrier) (*Circus cyaneus*) Montagu's Harrier (*Circus pygargus*) 7, d 165
Eurasian Kestrel (*Falco tinnunculus*) 6, d 10, 165, 196
Peregrine Falcon (*Falco peregrinus*) 6, d 23, 88
Short-eared Owl (*Asio flammeus*) 6, 7, d 10, 27, 165, 196

Montagu's Harrier (*Circus pygargus*) Short-eared Owl (*Asio flammeus*) 7, d 165

Marsh Harrier (<i>Circus aeruginosus</i>)	Marsh Hawk (Hen Harrier) (<i>Circus cyaneus</i>)	7, d	165
Bateleur (<i>Terathopius ecaudatus</i>)	Secretary Bird (<i>Sagittarius serpentarius</i>)	2, d	117
	Ground Hornbill (<i>Bucorvus</i> sp.)	2, d	117
Brown Harrier Eagle (<i>Circaetus cinereus</i>)	Bateleur (<i>Terathopius ecaudatus</i>)	6, d	41
Falconidae			
Northern Crested Caracara (<i>Caracara cheriway</i>)	Brown Pelican (<i>Pelecanus occidentalis</i>)	7, g	23, 88
(<i>Polyborus plancus</i>)	Crow (<i>Corvus</i> sp.)	6, d	23
Prairie Falcon (<i>Falco mexicanus</i>)	Marsh Hawk (<i>Circus cyaneus</i>)	6, d	24, 135
Lanner Falcon (<i>Falco biarmicus</i>)	Black-winged Kite (<i>Elanus caeruleus</i>)	2, d	152
Peregrine Falcon (<i>Falco peregrinus</i>)	European Sparrowhawk (<i>Accipiter nisus</i>)	7, d	117
	Marsh Hawk (<i>Circus cyaneus</i>)	6, d	23
	Eurasian Kestrel (<i>Falco tinnunculus</i>)	6, d	117
Northern Hobby (<i>Falco subbuteo</i>)	Eurasian Kestrel (<i>Falco tinnunculus</i>)	6, d	45
Merlin (<i>Falco columbarius</i>)	European Sparrowhawk (<i>Accipiter nisus</i>)	6, d	117
Red-footed Falcon (<i>Falco vespertinus</i>)	Eurasian Kestrel (<i>Falco tinnunculus</i>)	2, 8, d	84
Eurasian Kestrel (<i>Falco tinnunculus</i>)	Barn Owl (<i>Tyto alba</i>)	1, 7, s	58
	Little Owl (<i>Athene noctua</i>)	2, 7, 8, d	122
	Short-eared Owl (<i>Asio flammeus</i>)	2, 6, d	10, 37, 45, 48
Gruiformes			
Rallidae			
American Coot (<i>Fulica americana</i>)	Redhead (<i>Aythya americana</i>)	5, d, s	22
	Canvasback (<i>Aythya valisineria</i>)	5, d, s	22
Charadriiformes			
Charadriidae			
Spur-winged Lapwing (<i>Hoplopterus (Vanellus) spinosus</i>)	Gray-headed Gull (<i>Larus cirrocephalus</i>)	3, 5, d, s	173
Chionididae			
Snowy Sheathbill (<i>Chionis alba</i>)	King Penguin (<i>Aptenodytes patagonicus</i>)	4, 5, 10, d, s	× 197
	Adelie Penguin (<i>Pygoscelis adeliae</i>)	4, 5, 10, d, s	× 94, 197
	Chinstrap penguin (<i>Pygoscelis antarctica</i>)	4, 5, 10, d, s	× 94, 197
Black-faced Sheathbill (<i>Chionis minor</i>)	King Penguin (<i>Aptenodytes patagonicus</i>)	4, 5, 10, d, s	× 197
	Adelie Penguin (<i>Pygoscelis adeliae</i>)	4, 5, 10, d, s	× 197
	Chinstrap Penguin (<i>Pygoscelis antarctica</i>)	4, 5, 10, d, s	× 76, 197
Stercorariidae			
Great Skua (<i>Catharacta skua</i>)	Black-browed Albatross (<i>Diomedea melanophris</i>)	6, g	76
	Giant Fulmar (<i>Macronectes giganteus</i>)	6, 8, g	× 43
	White-chinned Petrel (<i>Procellaria aequinoctialis</i>)	6, g	× 76
	Wilson's Storm Petrel (<i>Oceanites oceanicus</i>)	6, 8, g, s	× 43
	Gannet (<i>Morus bassanus</i>)	6, 8, g	× 5, 64, 116, 117
	Blue-eyed Cormorant (<i>Phalacrocorax atriceps</i>)	6, 8, g	× 43
	Heron (<i>Ardea</i> sp.)	6, 8, g	× 5, 117
	Parasitic Jaeger (<i>Stercorarius parasiticus</i>)	6, d	64
	Herring Gull (<i>Larus argentatus</i>)	6, d, g	202
	Lesser Black-backed Gull (<i>Larus fuscus</i>)	6, d, g	202
	Kelp Gull (<i>Larus dominicanus</i>)	6, 8, g	× 43
	Great Black-backed Gull (<i>Larus marinus</i>)	6, d, g	202
	Gulls (<i>Larus</i> spp.)	6, 8, g	× 5, 117, 202
	Terns (<i>Sterna</i> spp.)	6, 8, g	× 5, 117, 202
	Razorbill (<i>Alca torda</i>)	6, d	× 64
	Common Murre (<i>Uria aalge</i>)	6, d	× 64
	Common Puffin (<i>Fratercula arctica</i>)	6, d	× 5, 7, 64

MacCormick's Skua (<i>Catharacta maccormicki</i>)	Blue-eyed Cormorant (<i>Phalacrocorax atriceps</i>)	6, d	×	197
Pomarine Jaeger (<i>Stercorarius pomarinus</i>)	Shearwaters (<i>Puffinus</i> sp.)	6, d, g	×	19
	Black-tailed Gull (<i>Larus crassirostris</i>)	6, d		128
	Glaucous Gull (<i>Larus hyperboreus</i>)	6, d, g	×	19, 202
	Iceland Gull (<i>Larus glaucoides</i> (<i>leucopterus</i>))	6, d, g	×	19, 202
	Black-headed Gull (<i>Larus ridibundus</i>)	6, d		128
	Herring Gull (<i>Larus argentatus</i>)	6, d		202
	Great Black-backed Gull (<i>Larus marinus</i>)	6, d		202
	Gulls (<i>Larus</i> spp.)	6, d, g	×	19
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	6, d, g	×	19, 128, 202
	Terns (<i>Sterna</i> spp.)	6, d, g	×	19
Parasitic Jaeger (Arctic Skua) (<i>Stercorarius parasiticus</i>)	Red-throated Loon (<i>Gavia stellata</i>)	7, d	×	111
	Northern Fulmar (<i>Fulmarus glacialis</i>)	6, 8, g	×	71, 74
	Shearwater (<i>Puffinus</i> sp.)	6, 8, g	×	91, 117
	Gannet (<i>Morus bassanus</i>)	2, g	×	147, 202
	Ivory Gull (<i>Pagophila eburnea</i>)	6, d	×	111
	Herring Gull (<i>Larus argentatus</i>)	6, 8, g	×	117, 166
	Glaucous Gull (<i>Larus hyperboreus</i>)	6, d		114
	Silver Gull (<i>Larus novaehollandiae</i>)	6, d		170
	Bonaparte's Gull (<i>Larus philadelphia</i>)	6, 9, d, g	×	19, 134
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	2, 6, 8, 9, d, g	×	7, 17, 19, 64, 71, 74, 111, 147, 166 202
	Common Tern (<i>Sterna hirundo</i>)	6, d	×	19, 134
	Arctic Tern (<i>Sterna paradisaea</i>)	6, 8, 9, d, g	×	7, 19, 64, 71, 74, 111, 166, 170
	Roseate Tern (<i>Sterna dougallii</i>)	6, d	×	19
	White-fronted Tern (<i>Sterna striata</i>)	6, 7, 9, d	×	55
	Bridled Tern (<i>Sterna anaethetus</i>)	6, d	×	170
	Least Tern (<i>Sterna albifrons</i>)	6, d	×	19
	Crested Tern (<i>Sterna bergii</i>)	6, d	×	170
	Razorbill (<i>Alca torda</i>)	6, d	×	17
	Thick-billed Murre (<i>Uria lomvia</i>)	6, d	×	17
	Common Murre (<i>Uria aalge</i>)	6, d	×	17
	Black Guillemot (<i>Cepphus grylle</i>)	6, d	×	17, 111, 202
	Common Puffin (<i>Fratercula arctica</i>)	1, 2, 6, 9, d	×	5, 7, 17, 64, 71, 74, 202
	Skylark (<i>Alauda arvensis</i>)	2, d	×	147
	Meadow Pipit (<i>Anthus pratensis</i>)	2, d	×	147
Long-tailed Jaeger (<i>Stercorarius longicaudus</i>)	Franklin's Gull (<i>Larus pipixcan</i>)	6, d	×	91
	Common Tern (<i>Sterna hirundo</i>)	6, d	×	134
	Black Tern (<i>Chlidonias niger</i>)	6, d	×	105
Laridae				
Heermann's Gull (<i>Larus heermanni</i>)	Gannet (<i>Morus bassanus</i>)	6, g		19
Black-tailed Gull (<i>Larus crassirostris</i>)	Brown Pelican (<i>Pelecanus occidentalis</i>)	s		19
	Streaked Shearwater (<i>Puffinus leucomelas</i>)	2, 7, d		128
	Japanese Cormorant (<i>Phalacrocorax capillatus</i>)	5, s		128
	Little Egret (<i>Egretta garzetta</i>)	7, s		128
	Black-headed Gull (<i>Larus ridibundus</i>)	2, 7, d		128
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	2, 7, d		128
	Common Tern (<i>Sterna hirundo</i>)	2, 7, d		128
	Rhinoceros Auklet (<i>Cerorhinca monocerata</i>)	2, 7, d		128
Audouin's Gull (<i>Larus audouinii</i>)	Common Shag (<i>Phalacrocorax aristotelis</i>)	7, d		51
Ring-billed Gull (<i>Larus delawarensis</i>)	Lesser Scaup (<i>Aythya affinis</i>)	2, 7, d		171
	Common Merganser (<i>Mergus merganser</i>)	6, 7, d		106
	Mergansers (<i>Mergus</i> sp.)	7, d		19
	American Coot (<i>Fulica americana</i>)	7, d		15
	Black-bellied Plover (<i>Pluvialis squatarola</i>)	6, d		136
	Dunlin (<i>Calidris alpina</i>)	6, d		136
	Bonaparte's Gull (<i>Larus philadelphia</i>)	6, d		136
	Arctic Tern (<i>Sterna paradisaea</i>)	2, d		63

Common (Mew) Gull (<i>Larus canus</i>)	Little Grebe (<i>Podiceps ruficollis</i>)	7, d	×	35, 117	
	Mallard (<i>Anas platyrhynchos</i>)	7, d, s		28	
	European Wigeon (<i>Anas penelope</i>)	7, d		163	
	Common Goldeneye (<i>Bucephala clangula</i>)	2, 7, d, s		28	
	Oldsquaw (<i>Clangula hyemalis</i>)	7, d, s		28	
	Common Merganser (<i>Mergus merganser</i>)	5, 7, d		29, 179	
	Red-breasted Merganser (<i>Mergus serrator</i>)	5, 7, d		103	
	European Coot (<i>Fulica atra</i>)	7, d		29	
	European Oystercatcher (<i>Haematopus ostralegus</i>)	6, 7, 8, 10, d		65, 67	
	Northern Lapwing (<i>Vanellus vanellus</i>)	6, 9, d		67, 96, 193	
	Eurasian Golden Plover (<i>Pluvialis apricaria</i>)	5, 6, 7, d		193	
	Redshank (<i>Tringa totanus</i>)	7, 8, d		77	
	Black-headed Gull (<i>Larus ridibundus</i>)	6, 7, d		3, 29, 67, 140, 184, 193	
	Caspian Tern (<i>Sterna caspia</i>)	6, 7, d		5*	
	Common Tern (<i>Sterna hirundo</i>)	6, 7, d		131	
	Least Tern (<i>Sterna albifrons</i>)	6, 7, d	×	184	
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	6, 7, d	×	184	
	Jackdaw (<i>Corvus monedula</i>)	2, 6, 7, d		4	
	Rook (<i>Corvus frugilegus</i>)	2, 6, 7, d		67	
	Fieldfare (<i>Turdus pilaris</i>)	2, 6, 7, d		67	
	Herring Gull (<i>Larus argentatus</i>)	Common Loon (<i>Gavia immer</i>)	7, d		99
		Common Shag (<i>Phalacrocorax aristotelis</i>)	4, 7, d, s		51, 117
		Whooper Swan (<i>Cygnus (Olor) cygnus</i>)	7, 8, 10, d		51, 95
Mallard (<i>Anas platyrhynchos</i>)		7, d, s	×	28	
Greater Scaup (<i>Aythya marila</i>)		2, d	×	180	
Oldsquaw (<i>Clangula hyemalis</i>)		7, d, s	×	28	
Common Eider (<i>Somateria mollissima</i>)		2, 7, d	×	28, 51, 90, 166, 180	
Black Scoter (<i>Melanitta nigra</i>)		2, 7, 8, d	×	163, 166	
Common Merganser (<i>Mergus merganser</i>)		2, 7, d, s	×	18, 28, 110, 133, 166	
Red-breasted Merganser (<i>Mergus serrator</i>)		2, 7, d, s	×	28, 62, 132	
Northern Lapwing (<i>Vanellus vanellus</i>)		6, 9, d		93	
Lesser Black-backed Gull (<i>Larus fuscus</i>)		6, 7, 8, d		190	
Common Gull (<i>Larus canus</i>)		6, 7, d		3, 184	
Black-headed Gull (<i>Larus ridibundus</i>)		6, d		69	
Least Tern (<i>Sterna albifrons</i>)		6, 7, d	×	184	
Sandwich Tern (<i>Thalasseus sandvicensis</i>)		6, 7, d	×	184	
Black Guillemot (<i>Cepphus grylle</i>)		2, d	×	28	
Common Puffin (<i>Fratercula arctica</i>)		5, 6, 8, d	×	46, 109, 127, 130, 155	
Lesser Black-backed Gull (<i>Larus fuscus</i>)		Mallard (<i>Anas platyrhynchos</i>)	7, d, s	×	28
		Common Eider (<i>Somateria mollissima</i>)	7, s	×	28
		Common Merganser (<i>Mergus merganser</i>)	2, 7, d		28, 132
		Red-breasted Merganser (<i>Mergus serrator</i>)	2, 7, d		28, 132
		Herring Gull (<i>Larus argentatus</i>)	6, 7, 8, 9, d		190, 191
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	6, g		166	
	Black Guillemot (<i>Cepphus grylle</i>)	7, s	×	28	
Common Puffin (<i>Fratercula arctica</i>)	6, 7, d	×	7, 46		
Western Gull (<i>Larus occidentalis</i>)	Brown Pelican (chicks) (<i>Pelecanus occidentalis</i>)	5, 8, g	×	19	
	Cormorant (<i>Phalacrocorax</i> sp.)	5, s	×	14	
Great Black-backed Gull (<i>Larus marinus</i>)	Arctic Loon (<i>Gavia arctica</i>)	2, d		28	
	Red-throated Loon (<i>Gavia stellata</i>)	2, d		28	
	Shearwater (<i>Puffinus</i> sp.)	6, d	×	78, 80	
	Gray Heron (<i>Ardea cinerea</i>)	7, g	×	78, 112	
	Mallard (<i>Anas platyrhynchos</i>)	7, d, s	×	28, 166	
	Northern Shoveler (<i>Anas clypeata</i>)	7, d		166	
	Greater Scaup (<i>Aythya marila</i>)	7, d		166	
	Tufted Duck (<i>Aythya fuligula</i>)	7, d	×	80, 166	
	Common Eider (<i>Somateria mollissima</i>)	2, 7, d	×	28, 90	
	Black Scoter (<i>Melanitta nigra</i>)	2, 8, d	×	166	
	European Coot (<i>Fulica atra</i>)	7, d	×	166	
	Common Gull (<i>Larus canus</i>)	6, 7, d		166	
	Herring Gull (<i>Larus argentatus</i>)	2, 6, g		1, 3, 184	

	Common Puffin (<i>Fratercula arctica</i>)	6, d	×	46, 78, 80, 130
Glaucous-winged Gull (<i>Larus glaucescens</i>)	Cormorant (<i>Phalacrocorax</i> sp.)	s		14
	Great Blue Heron (<i>Ardea herodias</i>)	5, 7, s		2*
	Mallard (<i>Anas platyrhynchos</i>)	2, 7, d, s		28
	Common Goldeneye (<i>Bucephala clangula</i>)	5, d		137
	Bald Eagle (<i>Haliaeetus leucocephalus</i>)	5, 7, s		2*
Glaucous Gull (<i>Larus hyperboreus</i>)	Northern Fulmar (<i>Fulmarus glacialis</i>)	6, d, g	×	19
	Common Eider (<i>Somateria mollissima</i>)	2, 6, 7, d	×	19, 90, 146
	Ivory Gull (<i>Pagophila eburnea</i>)	5, 6, d	×	111
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	6, d, g	×	19
	Razorbill (<i>Alca torda</i>)	6, d	×	19
	Black Guillemot (<i>Cephus grylle</i>)	6, d	×	19
Iceland Gull (<i>Larus glaucooides leucopterus</i>)	European Oystercatcher (<i>Haematopus ostralegus</i>)	2, 5, d		53
	Brown Pelican (<i>Pelecanus occidentalis</i>)	5, 10, s		9, 19, 20, 82, 88, 117
Laughing Gull (<i>Larus atricilla</i>)	Common Tern (<i>Sterna hirundo</i>)	6, 9, d		81, 82
	Arctic Tern (<i>Sterna paradisaea</i>)	6, 9, d		81, 82
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	4, 5, s		6, 81
	Black Skimmer (<i>Rynchops nigra</i>)	6, d		206
	Black-naped Tern (<i>Sterna sumatrana</i>)	6, 7, d		89
	Bridled Tern (<i>Sterna anaethetus</i>)	2, g		89
	Crested Tern (<i>Sterna bergii</i>)	4, 6, 7, 8, 9, d	×	89
	Lesser Crested Tern (<i>Sterna bengalensis</i>)	2, 4, 6, 7, 9, d		89
	Great Crested Grebe (<i>Podiceps cristatus</i>)	2, 7, d		28, 35, 79, 107, 131, 144, 163
Black-headed Gull (<i>Larus ridibundus</i>)	Little Grebe (<i>Podiceps ruficollis</i>)	2, 6, 7, d		193
	Manx Shearwater (<i>Puffinus puffinus</i>)	7, g		113, 163, 193
	Gray Heron (<i>Ardea cinerea</i>)	7, d, s		28, 166
	Mallard (<i>Anas platyrhynchos</i>)	7, d, s		166
	Northern Shoveler (<i>Anas clypeata</i>)	7, d		79
	Common Pochard (<i>Aythya ferina</i>)	7, d		166
	Greater Scaup (<i>Aythya marila</i>)	7, d		115, 117, 144, 160, 161, 166, 181
	Tufted Duck (<i>Aythya fuligula</i>)	7, 8, d		131, 181
	Common Goldeneye (<i>Bucephala clangula</i>)	2, 7, d		166
	Black Scoter (<i>Melanitta nigra</i>)	7, d		29, 131, 181
	Common Merganser (<i>Mergus merganser</i>)	7, d		103
	Red-breasted Merganser (<i>Mergus serrator</i>)	5, 7, d		144, 164
	Common Gallinule (<i>Gallinula chloropus</i>)	5, 7, d, s		29, 79, 117, 131, 144, 166, 181, 194
	European Coot (<i>Fulica atra</i>)	5, 6, 7, 9, d, s		
	European Oystercatcher (<i>Haematopus ostralegus</i>)	4, 5, 6, d, s	×	186, 193
	Northern Lapwing (<i>Vanellus vanellus</i>)	2, 5, 6, 7, 8, d	×	42, 57, 68, 77, 96, 105, 163, 169, 185, 193
	Eurasian Golden Plover (<i>Pluvialis apricaria</i>)	5, 6, 7, d		42, 77, 96, 193
	Black-tailed Gull (<i>Larus crassirostris</i>)	2, 7, d		128
	Common Gull (<i>Larus canus</i>)	6, g		166
	Black-legged Kittiwake (<i>Rissa tridactyla</i>)	2, 7, d		128
	Caspian Tern (<i>Hydroprogne caspia</i>)	7, s		98
	Common Tern (<i>Sterna hirundo</i>)	2, 3, 6, d		63, 128, 159, 181
	Least Tern (<i>Sterna albifrons</i>)	6, d		184
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	2, 3, 4, 5, 6, d		63, 159, 184, 189
	Razorbill (<i>Alca torda</i>)	7, d		138, 193
	Common Murre (<i>Uria aalge</i>)	7, d		193
	Carrion Crow (<i>Corvus corone</i>)	6, d		117
	Blackbird (<i>Turdus merula</i>)	s		42
	Redwing (<i>Turdus iliacus</i>)	s		42
	Fieldfare (<i>Turdus pilaris</i>)	s		42, 193
	Song Thrush (<i>Turdus philomelos</i>)	s		42
	Common Starling (<i>Sturnus vulgaris</i>)	5, 7, d		193
	Black-bellied Plover (<i>Pluvialis squatarola</i>)	6, d		136
Bonaparte's Gull (<i>Larus philadelphia</i>)	Dunlin (<i>Calidris alpina</i>)	6, d		136

Black-legged Kittiwake (<i>Rissa tridactyla</i>)	Arctic Tern (<i>Sterna paradisaea</i>)	6, d	111
	Common Puffin (<i>Fratercula arctica</i>)	6, d	7
Sabine's Gull (<i>Xema sabini</i>)	Arctic Tern (<i>Sterna paradisaea</i>)	6, d	134
Gulls (<i>Larus</i> spp.)	Cormorant (<i>Phalacrocorax</i> sp.)	s	14
	Tufted Duck (<i>Aythya fuligula</i>)	7, d	160
Gull-billed Tern (<i>Gelochelidon nilotica</i>)	Greenshank (<i>Tringa nebularia</i>)	6, d	153
Common Tern (<i>Sterna hirundo</i>)	Great Crested Grebe (<i>Podiceps cristatus</i>)	2, d	18, 28
	Diving Ducks (<i>Somateria</i> or <i>Aythya</i>)	7, d, s	28
	Arctic Tern (<i>Sterna paradisaea</i>)	6, 9, d	85
	Least Tern (<i>Sterna albifrons</i>)	6, d	134
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	6, d	189
Arctic Tern (<i>Sterna paradisaea</i>)	Horned Grebe (<i>Podiceps auritus</i>)	2, d	18
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	6, d	189
	Terns (<i>Sterna</i> spp.)	6, d	12
	Black Guillemot (<i>Cephus grylle</i>)	7, d	13
Roseate Tern (<i>Sterna dougallii</i>)	Common Tern (<i>Sterna hirundo</i>)	3, 5, 7, d, s	54
	Arctic Tern (<i>Sterna paradisaea</i>)	3, 5, 7, d, s	12, 54
	Black-naped Tern (<i>Sterna sumatrana</i>)	6, 7, 9, d	89
	Crested Tern (<i>Sterna bergii</i>)	6, 7, d	89
	Sandwich Tern (<i>Thalasseus sandvicensis</i>)	3, 5, 7, d, s	54
Brown Noddy (<i>Anous stolidus</i>)	Brown Pelican (<i>Pelecanus occidentalis</i>)	10, s	19, 117
Alcidae			
Razorbill (<i>Alca torda</i>)	Common Puffin (<i>Fratercula arctica</i>)	6, d	46
Strigiformes			
Strigidae			
Snowy Owl (<i>Nyctea scandiaca</i>)	Marsh Hawk (Hen Harrier) (<i>Circus cyaneus</i>)	1, s	52
Short-eared Owl (<i>Asio flammeus</i>)	Marsh Hawk (<i>Circus cyaneus</i>)	1, s	30
	Eurasian Kestrel (<i>Falco tinnunculus</i>)	1, s	151
Coraciiformes			
Alcedinidae			
Common Kingfisher (<i>Alcedo atthis</i>)	Dipper (<i>Cinclus cinclus</i>)	7, d	72
Meropidae			
Carmine Bee-eater (<i>Merops nubicus</i>)	Great Bustard (<i>Ardeotis arabs</i>)	10, s	120
Passeriformes			
Corvidae			
Florida Scrub Jay (<i>Aphelocoma coerulescens</i>)	Northern Mockingbird (<i>Mimus polyglottos</i>)	2, d	149
Black-billed Magpie (<i>Pica pica</i>)	Eurasian Kestrel (<i>Falco tinnunculus</i>)	8, 10, d	162
	Golden Eagle (<i>Aquila chrysaetos</i>)	7, 9, d	49
	Northern Shrike (<i>Lanius excubitor</i>)	13	102
Jackdaw (<i>Corvus monedula</i>)	Mallard (<i>Anas platyrhynchos</i>)	7, d, s	28
	Common Murre (<i>Uria aalge</i>)	5, 8, d	32, 33
	Common Puffin (<i>Fratercula arctica</i>)	5, 6, 8, d	46, 127, 155
Common Crow (<i>Corvus brachyrhynchos</i>)	Marsh Hawk (Hen Harrier) (<i>Circus cyaneus</i>)	6, d	23
	Herring Gull (<i>Larus argentatus</i>)	11	19
	American Robin (<i>Turdus migratorius</i>)	5, d	31
Hooded Crow (<i>Corvus cornix</i>)	Merlin (<i>Falco columbarius</i>)	6, d	187
	Eurasian Kestrel (<i>Falco tinnunculus</i>)	6, d	10
	Common Puffin (<i>Fratercula arctica</i>)	6, d	46
Carrion Crow (<i>Corvus corone</i>)	Gray Heron (<i>Ardea cinerea</i>)	6, g	117
	Black Kite (<i>Milvus migrans</i>)	6, 8, 9, d	70
	Eurasian Kestrel (<i>Falco tinnunculus</i>)	7, d	70
	Gulls (<i>Larus</i> spp.)	7, d	70
	Rook (<i>Corvus frugilegus</i>)	7, d	70
Australian Raven (<i>Corvus coronoides</i>)	Whistling Kite (<i>Haliastur sphenurus</i>)	6, 8, d	70
Common Raven (<i>Corvus corax</i>)	Common Puffin (<i>Fratercula arctica</i>)	4, 6, d	7

Paridae			
Great Tit (<i>Parus major</i>)	Marsh Tit (<i>Parus palustris</i>)	13	4*
Blue Tit (<i>Parus caeruleus</i>)	European Nuthatch (<i>Sitta europaea</i>)	13	3*
Mimidae			
Brown Thrasher (<i>Toxostoma rufum</i>)	American Robin (<i>Turdus migratorius</i>)	5, d	188
Turdidae			
Blackbird (<i>Turdus merula</i>)	Song Thrush (<i>Turdus philomelos</i>)	5, 12, d	123, 164, 175
	Redwing (<i>Turdus iliacus</i>)	5, d	164, 175
	House Sparrow (<i>Passer domesticus</i>)	5, d	175
	Chaffinch (<i>Fringilla coelebs</i>)	5, d	175
Fieldfare (<i>Turdus pilaris</i>)	Blackbird (<i>Turdus merula</i>)	5, d	175
Mistle Thrush (<i>Turdus viscivorus</i>)	Blackbird (<i>Turdus merula</i>)	5, d	1*, 175
	Song Thrush (<i>Turdus philomelos</i>)	5, d	1*
	Starling (<i>Sturnus vulgaris</i>)	5, d	1*
	House Sparrow (<i>Passer domesticus</i>)	5, d	1*
	Chaffinch (<i>Fringilla coelebs</i>)	5, d	1*
Laniidae			
Lesser Gray Shrike (<i>Lanius minor</i>)	Wheatear (<i>Oenanthe oenanthe</i>)	6, d	× 117
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	American Kestrel (<i>Falco sparverius</i>)	2, s	83
Fiscal Shrike (<i>Lanius collaris</i>)	Roller (<i>Coracias garrulus</i>)	7, d	× 121
Woodchat Shrike (<i>Lanius senator</i>)	Passerines	6, d	× 117
Sturnidae			
Common Starling (<i>Sturnus vulgaris</i>)	Blackbird (<i>Turdus merula</i>)	2, 5, d	38, 175
	Mistle Thrush (<i>Turdus viscivorus</i>)	5, d, s	1*, 34
	American Robin (<i>Turdus migratorius</i>)	5, d	31, 150, 188
Icteridae			
Boat-tailed Grackle (<i>Quiscalus (Cassidix) major</i>)	Glossy Ibis (<i>Plegadis falcinellus</i>)	2, 9, d, s	177
Ploceidae			
House Sparrow (<i>Passer domesticus</i>)	Winter Wren (<i>Troglodytes troglodytes</i>)	2, 4, d	36
	Blackbird (<i>Turdus merula</i>)	5, d	1*
	Mistle Thrush (<i>Turdus viscivorus</i>)	s	108
	American Robin (<i>Turdus migratorius</i>)	s	119, 139
	Starling (<i>Sturnus vulgaris</i>)	5, d	1*
Fringillidae			
Cardinal (<i>Cardinalis cardinalis</i>)	Loggerhead Shrike (<i>Lanius ludovicianus</i>)	13	198
Chaffinch (<i>Fringilla coelebs</i>)	European Nuthatch (<i>Sitta europaea</i>)	13	182

Index

1. Parasitic bird flies toward host and then rolls onto back and grabs prey directly from clutches of flying host.
2. Parasitic bird flies directly at host or pursues host over short distances.
3. Parasitic bird robs prey while host is presenting food to mate.
4. Parasitic bird robs food while host is feeding young.
5. Parasitic bird rushes at host who is on the ground or water.
6. Parasitic bird pursues host over long distances in chases.
7. Parasitic bird dives at host from above.
8. Parasitic bird physically contacts host by pecking, pulling feathers or hitting the host with the wings.
9. Several parasitic birds join together.
10. Parasitic bird sits on host's back or head.
11. Crows steal mussels which the gull has dropped on the ground (gulls drop mussels to break them open) (Bent 1921).
12. Blackbirds also steal snails that song thrushes have just opened by pounding on a rock (Morris 1954).
13. Parasite follows host around stealing food as host places food in a cache.
14. Food stolen as host manipulates it prior to eating.
15. Host takes prey from spider's web.
16. Frigatebirds steal nesting material as well as food from their hosts (Verner 1965; Diamond 1975).
- d. Parasitic bird picks up food dropped by host.
- g. Parasitic bird picks up food disgorged by host.
- s. Parasitic bird seizes prey directly from host.

1* Observations by C. J. Barnard, near Oxford, U.K., 1976-1978.

2* Observations by J. R. Krebs, near Victoria, British Columbia, Canada, 1972.

3* Observations by R. J. Cowie, Oxford, U.K., 1978.

4* Observations by J. Karlsson, Lund, Sweden, 1978.

5* Observations by Rolf Wahlin, Lund, Sweden.

APPENDIX B: A Review of Kleptoparasitism Between Birds and Mammals

Kleptoparasite*	Host*	Behaviour	Reference‡
Anseriformes			
Anatidae			
American wigeon (<i>Anas americana</i>)	Muskrat (<i>Ondatra zibethicus</i>)	5, 8, d, s	60
Falconiformes			
Accipitridae			
Common buzzard (<i>Buteo buteo</i>)	Stoat (<i>Mustela erminea</i>)	7, d	117
Lappet-faced vulture (<i>Torgos tracheliotus</i>)	Jackal (<i>Canis</i> sp.)	5, d	101
Kestrel (<i>Falco tinnunculus</i>)	Weasel (<i>Mustela</i> sp.)	7, d	56, 124
Galliformes			
Phasianidae			
Domestic chicken (<i>Gallus domesticus</i>)	Domestic cat (<i>Felis domesticus</i>)	5, s	160
Gruiformes			
Rallidae			
American coot (<i>Fulica americana</i>)	Muskrat (<i>Ondatra zibethicus</i>)	s	199
Charadriiformes			
Laridae			
Gulls (<i>Larus</i> sp.)	Seals (<i>Pinnipedia</i>)	14, s	117
Inca Tern (<i>Larosterna inca</i>)	Sea-lions (<i>Otaria byronia</i>)	14, s	126
Strigiformes			
Strigidae			
Short-eared owl (<i>Asio flammeus</i>)	Stoat (<i>Mustela erminea</i>)	7, d	204
Passeriformes			
Corvidae			
Clark's nutcracker (<i>Nucifragas columbiana</i>)	Red squirrel (<i>Tamiasciurus</i> sp.)	5, 7, d	26
Carrion Crow (<i>Corvus corone</i>)	Domestic dog (<i>Canis familiaris</i>)	5, d, s	70
Common Raven (<i>Corvus corax</i>)	Domestic dog (<i>Canis familiaris</i>)	5, d, s	26

Footnotes and index as per Appendix A.

Meinertzhagen (1959) reviews associations between birds and humans.

APPENDIX C: A Review of Kleptoparasitism Between Birds and Arthropods

Kleptoparasite*	Host*	Behaviour	Reference‡
Apodiformes			
Trochilidae			
Long-tailed hermit (<i>Phaethornis superciliosus</i>)	Spider's web	15	205
Green-breasted mango (<i>Anthracothorax prevostii</i>)	Spider's web	15	203
Steely-vented hummingbird (<i>Amazilia saucerotiei</i>)	Spider's web	15	203
Buff-bellied hummingbird (<i>Amazilia yucatanensis</i>)	Spider's web	15	195
Anna's hummingbird (<i>Calypte anna</i>)	Spider's web	15	25
Ruby-throated hummingbird (<i>Archilochus colubris</i>)	Spider's web	15	141, 203
Passeriformes			
Formicariidae			
Bicolored antbird (<i>Gymnopithys leucaspis</i>)	Army ants	s	200
Lunulated antbird (<i>Gymnopithys lunulata</i>)	Army ants	s	201
Pycnonotidae			
Bulbuls (<i>Pycnonotus</i> sp.)	Driver ants: (Formicidae: Dorylinae)	s	160
Troglodytidae			
White-bellied wren (<i>Uropsila leucogastra</i>)	Spider's web	15	195
Turdidae			
Alethe (<i>Alethe</i> sp.)	Driver ants: (Formicidae: Dorylinae)	s	160
American Robin (<i>Turdus migratorius</i>)	Digger wasp (Sphecidae: <i>Sphex</i>)	2, d	156
Bombycillidae			
Cedar waxwing (<i>Bombycilla cedrorum</i>)	Spider's web (Araneidae)	15	44
Sturnidae			
Starling (<i>Sturnus vulgaris</i>)	Digger wasp (Sphecidae: <i>Sphex</i>)	2, d	39
Vireonidae			
Yellow-green vireo (<i>Vireo flavoviridis</i>)	Spider's web	15	195
Parulidae			
Yellow-rumped warbler (<i>Dendroica coronata</i>)	Spider's web	15	195
Prairie warbler (<i>Dendroica discolor</i>)	Spider's web (Araneidae)	15	50
Icteridae			
Brown-headed cowbird (<i>Molothrus ater</i>)	Digger wasp (Sphecidae: <i>Sphex</i>)	2, d	39
Ploceidae			
House sparrow (<i>Passer domesticus</i>)	Digger wasp: (Sphecidae: <i>Sphex</i>)	2, d	39, 156
Fringillidae			
Blue bunting (<i>Cyanocompsa parellina</i>)	Spider's web (Araneidae)	15	195

Footnotes and index as per Appendix A.