

## CHAPTER 3

# Gyrffalcon and ptarmigan predator-prey relationship

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### 3.1 Introduction

The close predator-prey relationship between the Gyrffalcon and species of ptarmigan in the genus *Lagopus* has long been noted in the accounts of biologists and falconers, but the exact details of this relationship—just how and to what extent Gyrffalcons depend on ptarmigan for their food—require more study. Here we describe what is known and what can reasonably be inferred about this relationship.

Grouse (subfamily Tetraoninae) consist of medium to large size herbivorous birds found in deciduous and evergreen forests, and steppe and prairie biomes. Grouse originated in the New World where they split from a turkey-like ancestor 10–15 million years BP (see Persons et al. 2016 for details). One offshoot of this subfamily is the genus *Lagopus*, or ptarmigan, cold-adapted birds found in both Arctic and alpine tundra biomes. Presumably the stock ancestral to ptarmigan was a forest grouse, and this connection can still be seen in the dexterity shown by Rock Ptarmigan (*Lagopus muta*) when climbing trees. Three species of ptarmigan exist: Rock Ptarmigan, Willow Ptarmigan (*L. lagopus*), and White-tailed Ptarmigan (*L. leucura*). The Rock Ptarmigan and the Willow Ptarmigan have a Holarctic distribution, but the White-tailed Ptarmigan is confined to alpine areas in the western part of North America, the ancestral range of the genus (Persons et al. 2016). The split between the White-tailed Ptarmigan on the one hand and the stock ancestral to Rock Ptarmigan and Willow Ptarmi-

gan on the other, took place three to seven million years BP (Persons et al. 2016). The Rock Ptarmigan and the Willow Ptarmigan split two to five million years BP, most likely associated with the advent of the Pleistocene (Kozma et al. 2016, Persons et al. 2016). Climatic changes marking the start of the Pleistocene 2.6 million years BP created large expanses of open tundra (Huntley and Webb 2012). The Willow Ptarmigan and Rock Ptarmigan took advantage of this new habitat, dispersed widely, and have flourished ever since. The ptarmigan, being cold-adapted alpine birds, had pre-adaptations that facilitated the transition over to living on the tundra. Challenges in the new habitats were many, both biotic and abiotic; some were familiar while others were new. Abiotic factors included such things as harsh climate, short growing season, and few or no daylight hours in winter. Biotic factors included new food-web connections with respect to plant communities, competitors, parasites, and predators. A new predator-prey connection was made out on the tundra when ptarmigan met Gyrfalcons, another tundra newcomer but with different roots.

The Gyrfalcon belongs to the so-called hierofalcon complex along with the Saker Falcon (*Falco cherrug*), the Lanner Falcon (*F. biarmicus*), and the Laggar Falcon (*F. jugger*; Nittinger et al. 2005), and possibly the Australian Black Falcon (*F. subniger*; Fuchs et al. 2015). The hierofalcons are large predatory birds, adapted to hunt over open country and take prey both on the ground and in the air. They feed mainly on birds, mammals, and reptiles. The ancestral land of the hierofalcons is considered to be Africa, and from there separate waves of immigration into Eurasia and South Asia have taken place during the last million years (Nittinger et al. 2007, Fuchs et al. 2015). The Gyrfalcon and the Saker Falcon are closely related forms, usually considered allopatric species that share an immediate common ancestry. The Saker Falcon is confined to steppe and deserts in the Old World and the Gyrfalcon to the Arctic tundra and subarctic alpine habitats in the New and the Old Worlds (Cade 1982).

There is disagreement regarding when the split between the Gyrfalcon and the Saker Falcon occurred. One source places this event during the mid-Pleistocene 1 million years BP (Fuchs et al. 2015), but others after the last glacial maximum 24.5 thousand years BP (Potapov and Sale 2005; Johnson et al. 2007). Still other sources view the Saker Falcon and the Gyrfalcon as members of the same species (Cade 1982 and references therein).

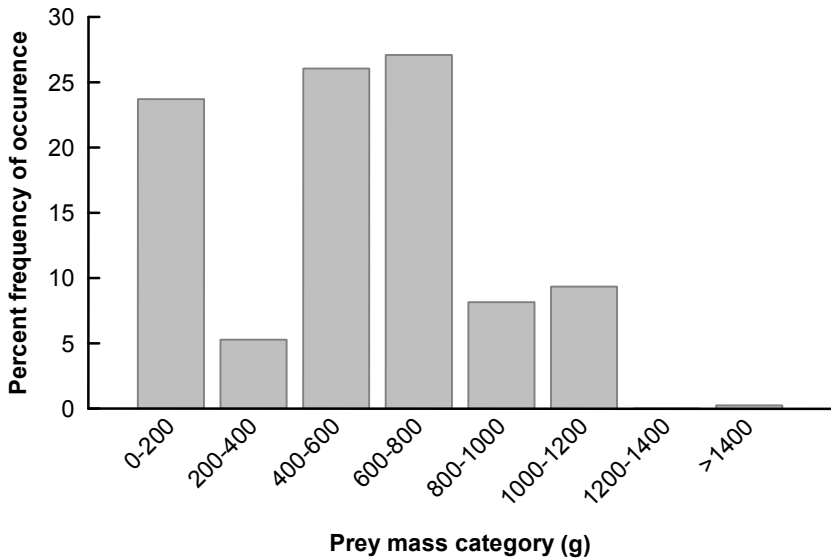
The Pleistocene has been characterized by repeated glacial events (termed glacials) when climate cooled and glaciers expanded and grew. The glacials were separated by interglacials with a more benign climate and the retreat or disappearance of glaciers. We are currently living in such an interglacial, the Holocene. At the height of the last glacial maximum a large fraction of the present range of the Gyrfalcon, Rock Ptarmigan, and Willow Ptarmigan in the Nearctic and Fennoscandia was covered with gla-

ciers (Huntley and Green 2011). The early Holocene must have been a period of major range expansion for the falcon and the ptarmigan from different glacial refugia (Holder et al. 1999, Johnson et al. 2007, Höglund et al. 2013). It seems likely that such events were repeated again and again during different glacials and interglacials further back in time. We assume that the Gyrfalcon-ptarmigan predator-prey relationship has existed on the tundra for a good part of the Pleistocene and the cat-and-mouse game played ever since has had consequences for all three species with respect to evolution, ecology, and population dynamics.

### 3.2 The raptor

The Gyrfalcon is the largest of the true falcons; males weigh 800–1,300 g and females 1,400–2,100 g (Cade 1982). It has a circumpolar breeding distribution, inhabiting polar deserts, tundra, alpine tundra, and the northern fringe of the taiga (Cade 1982). The Gyrfalcon is a powerful predator of both birds and mammals and versatile with respect to size of potential prey. In Iceland, Gyrfalcons regularly capture prey from the size of a Meadow Pipit (*Anthus pratensis*, body mass c. 20 g) up to an adult Pink-footed Goose (*Anser brachyrhynchus*, c. 2,500 g), a more than 100-fold difference in prey mass (Nielsen 2003). In the High Arctic, adult Arctic hares (*Lepus arcticus*) weighing up to 6 kg are sometimes taken, but more often Gyrfalcons take the smaller leverets (Cade and Bird 2011). The most common prey size in northeast Iceland—ignoring Rock Ptarmigan—are small birds (body mass less than 200 g), and medium size birds (400–800 g; Fig. 3.1).

The breeding distribution of the Gyrfalcon is completely contained within the breeding distribution of the Willow Ptarmigan and the Rock Ptarmigan (Fig. 3.2). There are no Gyrfalcon populations that do not share their breeding range with either one or both of the two ptarmigan species. However, there are breeding populations of both Willow and Rock Ptarmigan that do not share their ranges with breeding Gyrfalcons. For Rock Ptarmigan this exclusion includes some isolated alpine tundra populations (e.g., in Scotland, the Alps, the Pyrenees, Mongolia, and Japan) and insular Arctic populations (e.g., in Svalbard). For Willow Ptarmigan extensive breeding areas within the tundra-taiga ecotone in Europe and Siberia are without breeding Gyrfalcons (Voous 1960, Cramp and Simmons 1980). Some of the above-mentioned ptarmigan populations share winter habitats with Gyrfalcons, but others are more or less free from Gyrfalcon predation and have presumably been so at least since the end of the last glacial more than 10,000 years BP. One would expect that this continuum from ptarmigan populations that share their habitats with the Gyrfalcon during the annual cycle to ptarmigan populations that never suffer predation by a resident specialist predator like the Gyrfalcon should be reflected



**Figure 3.1** Percent frequency of Gyrfalcon prey size classes taken by falcons during spring and summer in northeast Iceland 1981–2016. Shown are results for prey other than adult and juvenile Rock Ptarmigan (*Lagopus muta*), in total 17,356 individuals of 63 species and 115 body mass categories based on age (adults versus young; Ó. K. Nielsen, unpubl. data).

in how their life histories have evolved through natural selection, a topic we discuss in more detail below.

### 3.3 The prey

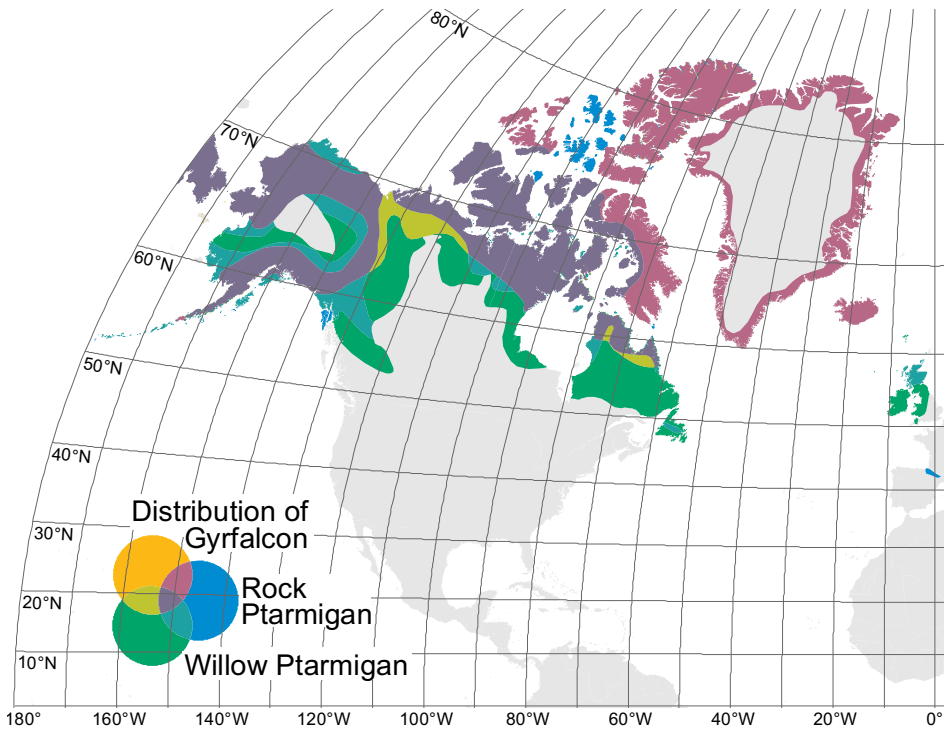
Willow Ptarmigan and Rock Ptarmigan are medium sized birds with similar build and that look alike, especially in winter plumage. The Rock Ptarmigan is the smaller of the two. Body size and mass varies across the range for both species. Rock Ptarmigan males commonly weigh 500–530g and females 420–480g, and Willow Ptarmigan males 580–650g and females 540–590g (Cramp and Simmons 1980, Watson and Moss 2008). Both species are found mainly in open and exposed Arctic, subarctic, and Arctic-alpine habitats. The Rock Ptarmigan reaches farther north than the Willow Ptarmigan and is confined to more open and exposed areas, whereas the Willow Ptarmigan prefers higher shrub cover. They are both strictly herbivorous apart from small chicks that include invertebrates in their diet. Important winter foods are buds, twigs, and catkins of various species of dwarf shrubs. Willow Ptarmigan and Rock Ptarmigan compete for both space and food where sympatric (Moss 1974). Under such conditions, the Rock Ptarmigan occupies higher and more exposed areas than

Willow Ptarmigan and feeds more on buds, catkins, and twigs of *Betula* spp. and less on *Salix* spp. than the Willow Ptarmigan (Weeden 1969, Moss 1974, Thomas 1984). Both species are essentially resident within their breeding range but some northerly populations, particularly of Willow Ptarmigan, move southward in winter to riparian areas in river valleys or to the tundra-taiga ecotone (Cramp and Simmons 1980, Watson and Moss 2008).

Many populations of both Rock and Willow Ptarmigan have cyclic population dynamics characterized by regular cyclic changes of numbers. The length of the cycle differs: it can be as short as three to four years for Willow Ptarmigan in Norway (Hagen 1952a) and approximately six years for the same species in Scotland (Jenkins et al. 1967). More commonly the cycle length is 10–12 years as for Willow Ptarmigan in Siberia (Andreev 1988) and Yukon (Mossop 2011), and Rock Ptarmigan in Iceland (Nielsen and Pétursson 1995), Scotland (Watson et al. 1998), and Alaska (Weeden and Theberge 1972). The difference in spring numbers between high and low years is commonly 3–5-fold but can be up to 20–30-fold (Nielsen 1999b, unpubl. data). Such cycles are known for different species of herbivores in boreal and Arctic areas, including birds (grouse), mammals, and invertebrates. This phenomenon has long captured the imagination of ecologists (Elton 1924, Keith 1963). What drives these cycles has been argued, but the focus has been on trophic interactions such as herbivore-plant (Bryant 1981), parasite-host (Hudson et al. 1998, Myers and Cory 2013), predator-prey (Korpimäki and Krebs 1996), or some combination of these factors (Krebs et al. 2001). For predator-prey interaction the attention has been on the nature of the relationship and distinction made based on how the predator responds to changes in prey numbers. Predators that respond in a delayed density-dependent fashion to changes in prey number are thought to play a role in cyclic prey dynamics (Murdoch and Oaten 1975).

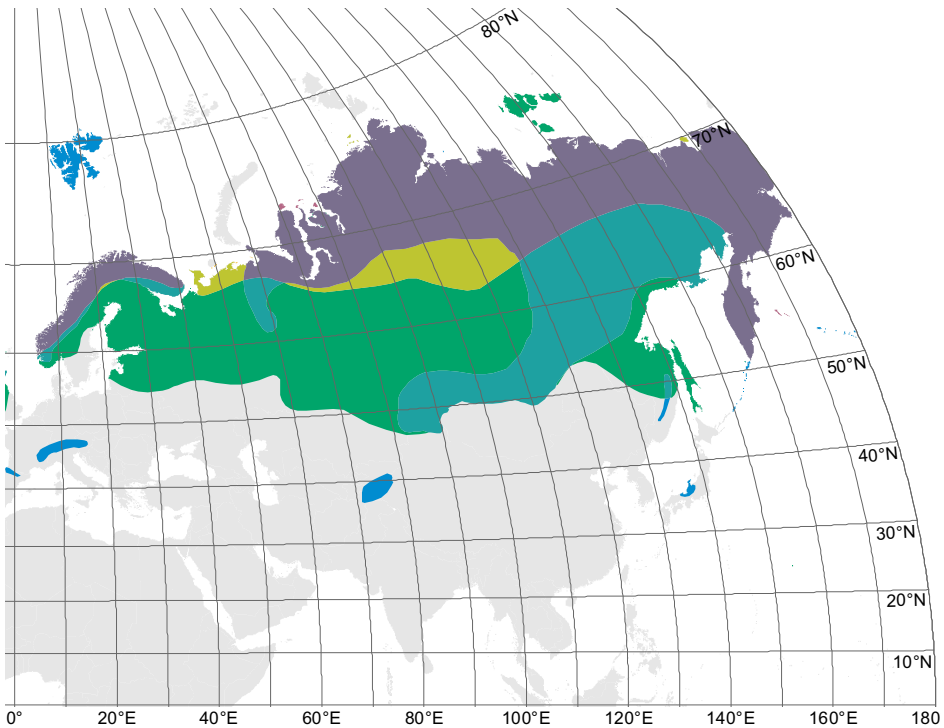
### 3.4 Importance of ptarmigan in Gyrfalcon diet

How important are Rock and Willow Ptarmigan as prey for the Gyrfalcon? The falcons start to bring prey to the nesting cliff at the onset of courtship in late winter, and if the nesting attempt is successful this will continue until the nestlings disperse some 140 days later (Nielsen 2003). Most students of Gyrfalcon ecology have used this behavior to study the food habits of the falcon mainly by collecting prey remains and cast pellets at occupied nests (Cade et al. 1998, Potapov and Sale 2005, Booms et al. 2008). We have selected some 17 studies, where number of identified prey is greater than 300 individuals, to compare feeding habits of nesting Gyrfalcons across regions (Table 3.1). The limit is completely arbitrary but we want to concentrate the attention to studies that at least cover several nesting



**Figure 3.2** Breeding distribution of Gyrfalcon (*Falco rusticolus*), Rock Ptarmigan (*Lagopus muta*), and Willow Ptarmigan (*Lagopus lagopus*).

territories or several years for one nesting territory. All the data we use except one set are based on collection of prey remains or some combination of remains and pellets. Robinson (2016) used data derived from motion-activated nest cameras. It should be noted that diet studies using prey remains may be distorted by potential biases (Booms and Fuller 2003, Robinson 2016), but these can be reduced if collections are done in a standardized way (Nielsen 2011). Prey remains are easy to collect when doing other field work and can tell an interesting story relating both to the life history and the population dynamics of the falcon (Fig. 3.3, but see also Nielsen 1999a, 2003). Further, nest cameras give detailed information but thus far have only been used to study the nestling period (approximately 49 days or about 35% of the entire breeding season) because food is not delivered to the nest during courtship and incubation and post-fledging period (Cade et al. 1998). Food remains, if collected in a systematic way, will cover the entire breeding period from start of courtship into the post-fledge period (Nielsen 1999a, Nielsen 2011).



The Venn diagram illustrates the separate and overlapping ranges of the three species. Based on Voous (1960) and Cramp and Simmons (1980).

The 17 study areas are not evenly spread across the range of the Gyrfalcon (Table 3.1). Eight of them are in northeast Europe, Fennoscandia (Norway, Sweden, and Finland) and the Kola Peninsula (Russia). Five areas are in Alaska, two are in Nunavut, Canada (in the central Arctic mainland and on Ellesmere Island in the High Arctic), and one each in Greenland and Iceland. Obvious gaps are in Siberia and parts of the Canadian Arctic and Greenland. There are some data available from these regions but sample sizes are small; these studies will be referred to as appropriate below.

In total 66,726 prey individuals and at least 130 species were identified. In our analysis we summarized the prey into 11 groups and used percentage by biomass to express their importance (Table 3.1). Ptarmigan were the dominant prey in all studies but one, but their importance seemed to vary somewhat by region. In Fennoscandia and on the Kola Peninsula ptarmigan scored high, average 85% biomass (range 67–99%). In Alaska, Nunavut, Greenland, and Iceland, ptarmigan averaged 71% biomass

**Table 3.1** Food habits of the Gyrfalcon during the breeding season in different geographic areas. Prey species are ordered into 11 groups and importance in diet is expressed as percent by biomass.

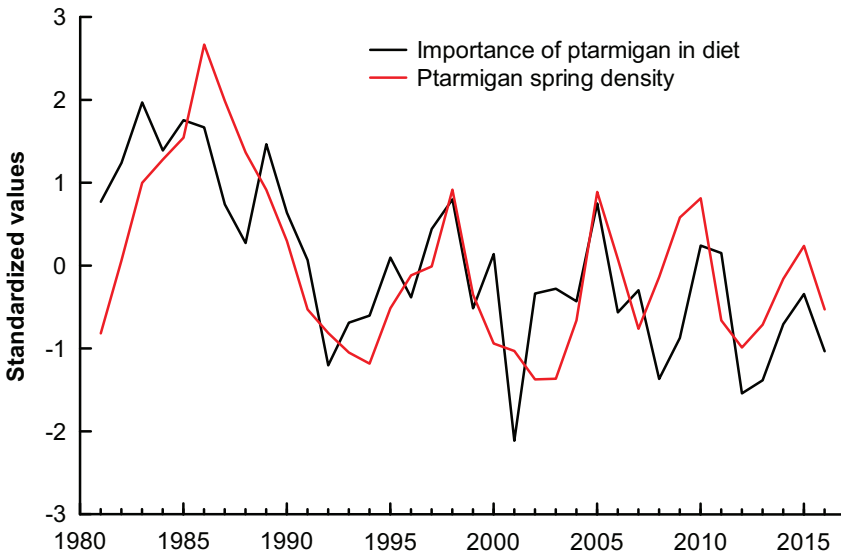
Region	Ptarmigan	Water-fowl	Shore-birds	Alcids	Gulls, skuas, terns	Passerines	Other birds
Yukon-Kuskokwim Delta, Alaska (62°N)	95.7	2.1	0.1	...	...	0.1	1.8
Alaska Range (64°N)	44.5	0.8	0.3	...	0.2	0.1	0.5
Seward Peninsula, Alaska (65°N)	71.6	1.7	1.7	1.0	7.5	0.2	0.5
Seward Peninsula, Alaska (65°N)	52.1	0.3	6	<0.1	1.5	1.5	1.5
Colville River, Alaska (69°N)	94.1	2.5	0.1	...	0.6	<0.1	1
Northwest Territories (68°N)	73.2	2.3	0.1	...	...	0.6	...
Ellesmere Island (78°N)	2.9	0.1	8.4	...	...	0.4	0.6
W-Greenland (67°N)	71.7	9.0		...	...	0.3	...
NE-Iceland (65°N)	66.5	23.3	3.3	6.0	0.7	0.1	0.1
Hardangervidda, Norway (60°N)	91.0	...	<0.1	...	...	1.2	3.7
Trøndelag, Norway (64°N)	90.5	0.5	1.1	...	...	3.1	1.9
Finnmark, Norway (69°N)	98.2	0.2	0.8	...	0.1	0.3	0.3
Norrbottnen, Sweden (66°N)	98.9	...		...	...		0.4
Norrbottnen, Sweden (67°N)	82.9	2.4	0.5	<0.1	0.3	2	4.2
Forest Lapland, Finland (68°N)	70.9	2.5	9.4	...	0.3	1.7	13.7
N-Finland (69°N)	88.8	1.5	3.0	...	0.3	1.1	4.4
Kola Peninsula, Russia (69°N)	67.7	4.7	2.6	1.7	9.5	0.7	2.9

We calculated biomass values for Haftorn (1971), White and Cade (1971) and McCaffery et al. (2011). We did not use two data sets with more than 300 prey from NE-Iceland (Bengtson 1971, Woodin 1980) as they come from the same area we present. Also we choose to use data from



Rodents	Hares	Arctic Ground Squirrel	Other	N	Collections (years)	Source
<0.1	0.2	...	<0.1	444	16 (4)	(McCaffery et al. 2011)
0.3	...	52.5	0.8	305	4 (2)	(Bente 1981)
0.4	...	15.4	0.1	1,481	40 (3)	(Roseneau 1972)
0.4	...	36.19	0.5	2,008	20 (2)	(Robinson 2016)
0.2	...	1.5	...	618	27 (3)	(White and Cade 1971)
0.5	9.7	13.6	...	1,003	7+ (3)	(Poole and Boag 1988)
5.1	82.3	...	0.2	732	3 (3)	(Muir and Bird 1984, Cade and Bird 2011)
...	18.0	...	1.0	1,035	22 (2)	(Booms and Fuller 2003)
<0.1	...	...	<0.1	52,125	607 (36)	Nielsen unpubl. data 1981–2016
2.6	1.3	...	0.2	887	? (11)	(Hansen 1999)
0.3	2.4	...	0.2	437	5 (4)	(Langvatn and Moksnes 1979)
...	...	...	0.1	1,252	Not given	(Haftorn 1971)
0.7	...	...	...	406	13 (4)	(Nyström et al. 2006)
4.6	2.7	...	0.4	1,410	22 (12)	(Lindberg 1983)
0.3	1.2	...	<0.1	729	10 (9)	(Huhtala et al. 1996)
0.1	0.6	...	0.1	1,153	27 (5)	(Koskimies and Sulkava 2002)
5.4	3.2	...	1.6	702	8 (4)	(Kishchinskiy 1957)

Koskimies and Sulkava (2002) rather than a more extensive data set from the same region and the same authors (Koskimies and Sulkava 2011) because the latter did not include biomass calculations.



**Figure 3.3** The relationship between the Rock Ptarmigan (*Lagopus muta*) spring population index and the importance of ptarmigan in Gyrfalcon (*Falco rusticolus*) diet in northeast Iceland 1981–2016. Based on food remains collected at 607 nests where nestlings fledged successfully. In total 52,125 prey individuals identified (Ó. K. Nielsen, unpubl. data). The time series were standardized to zero mean and unit variance.

(range 45–96%). Other prey, or what we call alternative prey, were waterfowl (max. 23% biomass in Iceland), shorebirds (max. 9% biomass in Lapland), passerines (max. 3% biomass in Trøndelag, Norway), alcids (max. 6% biomass in Iceland), gulls, skuas, and terns (max. 10% biomass on Kola Peninsula), and Arctic ground squirrel (*Spermophilus parryii*; max. 53% biomass in Alaska).

The only data that suggest that there are Gyrfalcon populations with main food-web connections to prey other than ptarmigan are from Ellesmere Island, but the data are limited and come mainly from one nest site (Muir and Bird 1984, Cade and Bird 2011). These birds subsisted primarily on Arctic hares (82% biomass) during most of the breeding season, and to a lesser extent also on shorebirds (8% biomass), collared lemmings *Dicrostonyx groenlandicus* (5% biomass), and Rock Ptarmigan (3% biomass). It is not known how representative these results are for Gyrfalcons in the Canadian High Arctic. There is also information from the Greenland High Arctic where Gyrfalcons are perhaps uncoupled from the Rock Ptarmigan through their trophic relation with the Little Auk (*Alle alle*; Burnham 2007). Also, there are data from northeast Greenland that suggest that the Gyrfal-

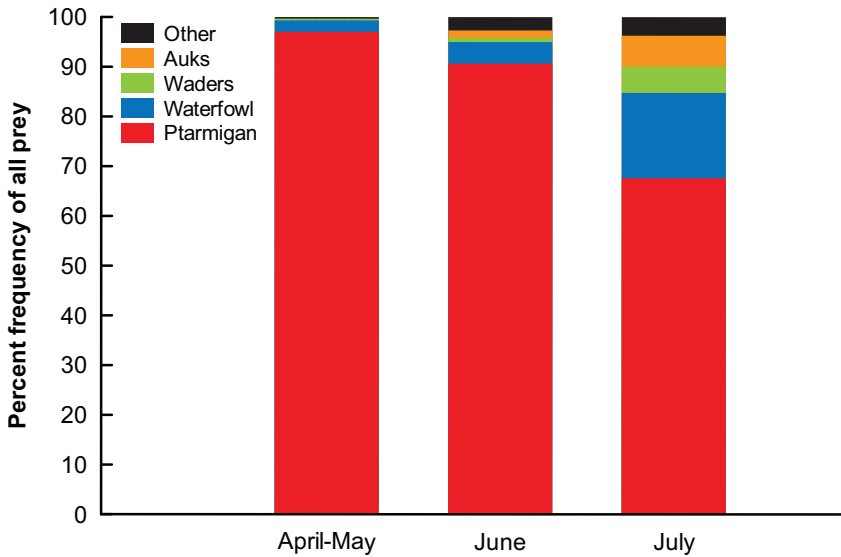
con and the Collared Lemming have a coupled predator-prey relationship where the Gyrfalcon may show both a numerical and a functional response to changes in lemming numbers (Gilg et al. 1997), again based on observations of a single nest site. Other important prey for the Gyrfalcon in that region are Rock Ptarmigan, Arctic hares, shorebirds and Snow Buntings (*Plectrophenax nivalis*; Summers and Green 1974, Fletcher and Webby 1977, Cabot et al. 1988). In none of these cases is it known for certain that ptarmigan are not being preyed upon in the early part of the breeding season. Apart from the above examples, all other Gyrfalcons that have been studied in any detail begin their breeding by feeding on ptarmigan and continue to do so as long as they remain available.

### 3.5 Importance of ptarmigan in Gyrfalcon diet during the annual cycle

To further our understanding of the relationship between the Gyrfalcon and ptarmigan it is important to describe the chronological changes both in prey composition, age, and sex of ptarmigan hunted over the course of the breeding season. The reason is the length of the Gyrfalcon's breeding season, because much changes with respect to the vulnerability of ptarmigan as prey for the falcons during this time.

All studies on Gyrfalcon food habits that cover the early phase of the breeding season (courtship to hatching of nestlings) show that ptarmigan are almost the only prey brought by the male to the nest site (Bengtson 1971, Woodin 1980, Bente 1981, Poole and Boag 1988, Nielsen 2003, Barichello 2011). There is no area within the entire breeding range where Gyrfalcons are known to feed consistently on prey other than ptarmigan up to about the time of egg-hatching, even in those populations that have an opportunity to switch to alternative prey. Thus, it appears essential for ptarmigan to be present in sufficient numbers for Gyrfalcons to initiate laying. In Iceland, the importance of ptarmigan starts to diminish in the early- or mid-nestling period (Fig. 3.4).

The falcons take proportionally more male than female ptarmigan in spring, at least in Iceland. In northeast Iceland the average percentage of Rock Ptarmigan males caught in April–May was 63% (95% CL  $\pm$  4%, n=446), and 59% in June (95% CL  $\pm$  4%, n=446; Nielsen 2003). Sex ratio in this ptarmigan population is equal in spring (Gardarsson 1988). The dominance of males in the diet is likely related to their white plumage and frequent territorial ground displays (MacDonald 1970). Barichello and Mossop (2011) have hypothesized that juvenile (first year) ptarmigan are preferred by the falcons over adults (second year or older), and that the breeding success of Gyrfalcons depends heavily on what proportion of the spring ptarmigan population is yearlings. This is an interesting hypothesis and should be tested.



**Figure 3.4** Seasonal changes in composition of the main prey groups in Gyrfalcon (*Falco rusticolus*) diet in northeast Iceland, 1987. Adapted from Nielsen (2003).

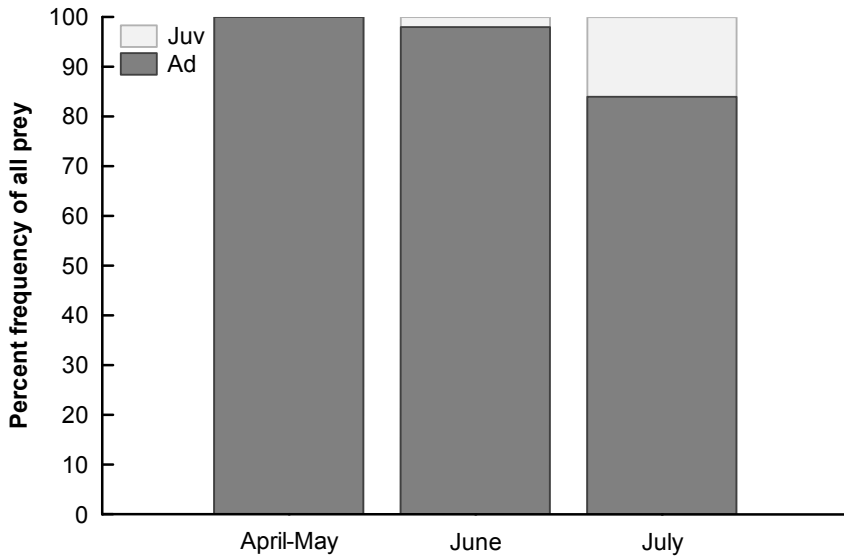
The switch over to prey other than ptarmigan starts in June in Iceland and the alternative prey are usually most prevalent at the end of the nestling period in July (Fig. 3.4). In the central Canadian Arctic, the switch to juvenile Arctic ground squirrels occurred immediately after their emergence around the first of July (Poole and Boag 1988). What species are taken as alternative prey depends on which are present (Table 3.1). It is important to note that ptarmigan will continue to be taken to the end of the breeding season as long as they are available (Poole and Boag 1988, Booms and Fuller 2003, Nielsen 2003, Robinson 2016). Midsummer predation is again directed mainly at adult ptarmigan, but at least in Iceland concentrated mostly on females, a complete reversal from the situation in spring and early summer. The increase in vulnerability of females over males is most likely driven by distorted sex ratio and difference in sex role. Female ptarmigan alone lead and defend broods and are easier to find than the now secretive males. The average percentage of Rock Ptarmigan females in the Gyrfalcon catch in July in northeast Iceland was 70% (95% CL  $\pm$  3%,  $n=890$ ; Nielsen 2003). In northeast Iceland Rock Ptarmigan chicks only appeared in the diet when they were approximately four weeks old, and this prey was most prevalent after fledging of the Gyrfalcon nestlings in the latter part of July. Other studies have shown similar results and do not report ptarmigan chicks as important in diet (see references in Table 3.1). Actually, this heavy reliance during the breeding season on

adult prey in general is one of the peculiarities of the Gyrfalcon as noted by Hagen (1952b) and Cade (1960). The Gyrfalcon is able to secure its reproductive output by preying mainly on the mature segments of its prey populations during their annual low in numbers (Fig. 3.5).

Winter diet depends on where the Gyrfalcons reside. The breeding territory, basically the nesting cliff and its immediate surroundings, is central in the life of the adult Gyrfalcon. These territories are traditional, being used generation after generation (Burnham et al. 2009), and the falcons will fight conspecifics for ownership (Nielsen and Cade 1990b). We assume that established territorial Gyrfalcons stay on their territories all year if possible. Such was the pattern observed in northeast Iceland and similar results are known from Alaska, USA (Bente 1981, Eisaguirre et al. 2016), and Finnmark, Norway (A. Östlyngen unpubl. data). Eisaguirre et al. (2016) observed home range size for two adult Gyrfalcon females over winter in Alaska. In Yukon (Platt 1976) and Nunavut, Canada (Poole and Bromley 1988), Gyrfalcons were present on territories at least from February.

Feasibility of winter residence in breeding areas should be determined largely by local prey availability and also to some extent on light conditions. Even in Finnmark beyond 70°N and where the sun remains under the horizon for two months or more, at least some adult Gyrfalcons stay on their territories during the winter (A. Östlyngen unpubl. data). This suggests that Gyrfalcons can forage during the Arctic night. Supporting this is an observation from Iceland in winter of a Gyrfalcon chasing ptarmigan during the night (Gunnlaugsson 1970), and observations by falconers who have lost Gyrfalcons while hunting and seen them return home well after dark (T. Cade, pers. obs.). At inland Gyrfalcon sites across the breeding range the only common prey in winter are ptarmigan and occasionally hares. All migrant birds have left, Arctic ground squirrels are hibernating, and microtines are living their lives below the snow. In such situations one would expect that the main prey of the falcon in winter would be ptarmigan. It should be noted that Gyrfalcons readily feed on carrion and this habit could facilitate wintering within the Arctic (Tömmereas 1989, Nielsen 2002).

Some Gyrfalcon populations such as in Arctic Greenland are migratory, including both juvenile and adult birds (Burnham and Newton 2011). Also, we know from satellite tracking of juvenile Gyrfalcons in Alaska (McIntyre et al. 2009, Eisaguirre et al. 2016) and Sweden (Nygård et al. 2011) that this cohort can be migratory or disperse long distances. The infrequent migratory adults are usually females (see Booms et al. 2008 and references cited therein). Migratory Gyrfalcons wintering beyond the range of ptarmigan subsist on a variety of prey such as alcids, waterfowl, pigeons, other gallinaceous birds, and shorebirds (Jenning 1972, Garber et al. 1993,



**Figure 3.5** Importance of adults and nestlings of all avian prey species in Gyrfalcon (*Falco rusticolus*) breeding season diet, northeast Iceland, 1987. Adapted from Nielsen (Nielsen 2003).

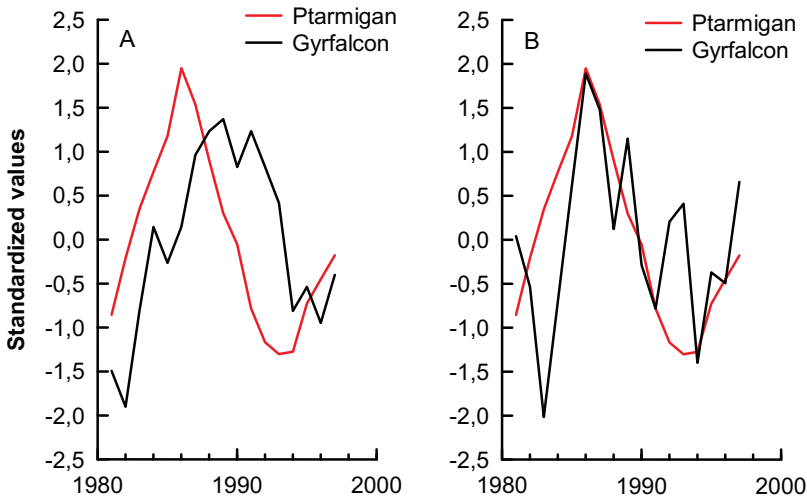
Sanchez 1993, Dekker and Lange 2001, Dekker and Court 2003, Burnham and Newton 2011, Castelijnns 2012).

We know of only one study, based on collection and analysis of pellets, where the food habits of resident Gyrfalcons were followed systematically over the non-breeding season (Nielsen and Cade 1990a). This was in northeast Iceland and covered Gyrfalcons living on the coast (coastal-falcons), at wetland areas inland (lakeland-falcons), and inland away from wetland areas (heathland-falcons). It was known from analysis of prey remains collected at nest sites during the breeding season in this area that alternative prey for the coastal-falcons were mainly alcids, for lakeland-falcons waterfowl, and shorebirds and waterfowl for heathland-falcons (Nielsen 1986). Pellet studies showed that the importance of Rock Ptarmigan increased again in late summer and into autumn for all falcons after a midsummer low, and then the predation was directed at the young of the year. Heathland-falcons continued all through winter by preying mainly on ptarmigan. Lakeland-falcons increased their take of waterfowl in winter, and coastal-falcons theirs of waterfowl and alcids.

### 3.6 Predator-prey relationship: a case study from Iceland

The nature of the connection between the Gyrfalcon and the ptarmigan will depend on whether the two are sympatric or not over the annual cycle. We expect to observe a continuum between two extremes regarding the role of the falcon as a predator of ptarmigan. On the one end are regions where populations of both resident ptarmigan and Gyrfalcons occur, and on the other end are regions where migratory Gyrfalcons occur, and the local ptarmigan populations only suffer Gyrfalcon predation from early spring until the end of fall. In the first case one would expect the Gyrfalcon to function as a “resident specialist predator” with respect to the ptarmigan, but in the second case more as a “generalist predator” (Andersson and Erlinge 1977). In each case we expect the population consequences for the ptarmigan would be different. Sharing the habitat with a resident, specialist predator should promote instability in population dynamics, but sharing the habitat with a generalist predator should promote stability (Andersson and Erlinge 1977, Turchin 2003). There are not many studies that have addressed the predator-prey relationship of Gyrfalcon and ptarmigan. To be able to do any assessment of the nature of the relationship one must have a valid index of numbers for both prey and predator, falcon fecundity, and diet composition. Further, the time series should be long enough so that a statistical comparison can be made, following the rule of thumb that a series is three times the cycle length (Turchin 2003). The only study that fulfills all these requirements is from northeast Iceland from 1981 to 2016 ( $n=36$  years; Nielsen 1999a, 2003). We used this study and data from 1981–1997 as our baseline to describe the numerical and the functional response of the Gyrfalcon to changes in ptarmigan numbers. There are also other studies that address this issue at least partly, including studies from Yukon (Mossop and Hayes 1994, Mossop 2011), Greenland (Burnham and Burnham 2011), Nunavut (Shank and Poole 1994), Finnmark, Norway (Tömmerraas 1993, Johansen and Östlyngen 2011), and Finland (Koskimies 2011).

The numerical response of Gyrfalcons in northeast Iceland, expressed as the number of territorial pairs in relation to changing Rock Ptarmigan densities, suggests that the two species have a coupled predator-prey cycle. The two populations rise and fall in unison but the falcon with an approximately three-year time-lag (Fig. 3.6a). The total number of falcon nestlings fledged, another measure of the numerical response, changed in synchrony with ptarmigan numbers (Fig. 3.6b). The numerical response as expressed in the number of territories occupied is due to changes in fecundity, mortality, and the balance between immigration and emigration (Solomon 1949). High site fidelity of adult Gyrfalcons in Iceland, productivity related to Rock Ptarmigan numbers, and late maturation should



**Figure 3.6** The numerical response of Gyrfalcon (*Falco rusticolus*) to changes in Rock Ptarmigan (*Lagopus muta*) numbers, northeast Iceland, 1981–1997. Time series were standardized to zero mean and unit variance. Ptarmigan data are spring density of territorial males. Gyrfalcon data are A) number of occupied territories and B) total number of young fledged. Adapted from Nielsen (1999a).

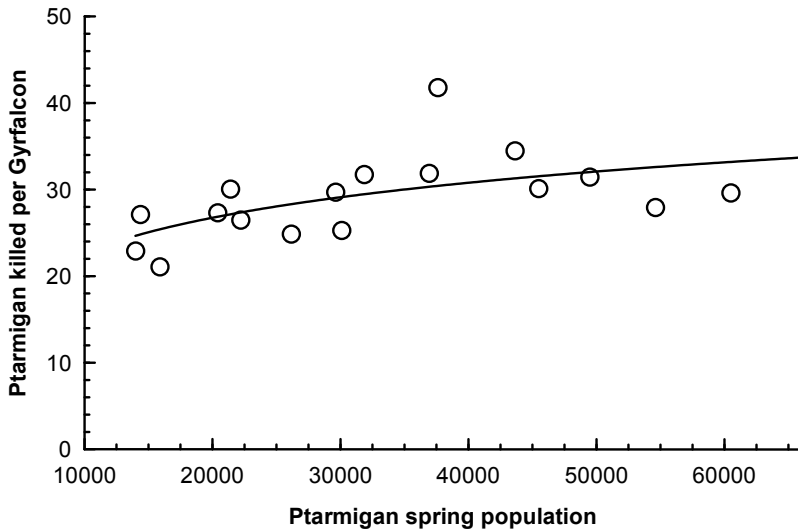
promote a slow numerical response and the number of falcon territories occupied should lag behind changes in ptarmigan numbers.

The functional response is expressed as the change in capture rate in response to changing prey density (Solomon 1949). The shape of the Gyrfalcon's functional response curve over the breeding season was determined by how much the falcons shifted over to alternative prey. This change depended on ptarmigan numbers, not on the number of alternative prey. The importance of ptarmigan in Gyrfalcon diet and ptarmigan numbers changed in synchrony (Fig. 3.3). The functional response of the Gyrfalcon was close to linear or slightly concave (Fig. 3.7), reminiscent of what is called Type 2 functional response where intake rate decelerates with increasing density of prey (Holling 1959).

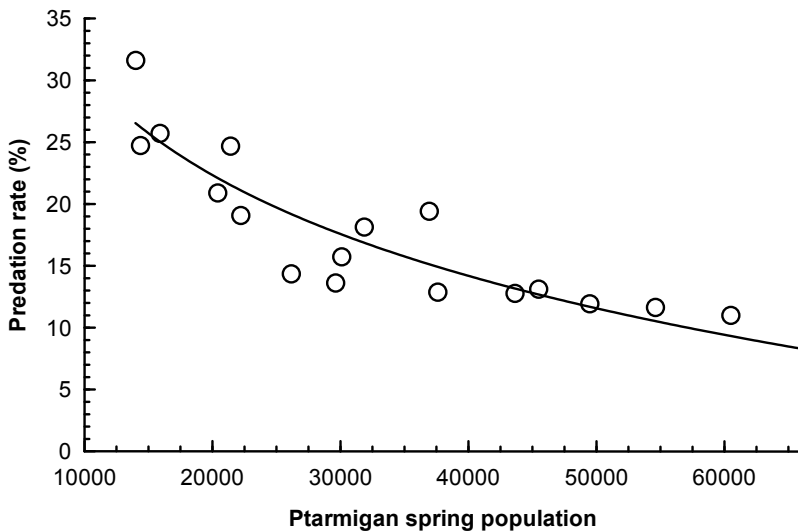
The total response to changing Rock Ptarmigan numbers is calculated by multiplying the functional and the numerical response and can be expressed as kill rate (total number killed) or predation rate (proportion of prey population killed). The predation rate shows how the proportion of Rock Ptarmigan killed by Gyrfalcons declined with increasing ptarmigan population (Fig. 3.8).

It should be noted that the food web in Iceland is relatively simple. The Rock Ptarmigan is the dominant wild vertebrate herbivore and a key-





**Figure 3.7** Functional response of Gyrfalcon (*Falco rusticolus*) during breeding season to variation in Rock Ptarmigan (*Lagopus muta*) spring numbers in northeast Iceland 1981–1997. Adapted from Nielsen (1999a). The fitted trend line is a logarithmic function.



**Figure 3.8** Spring and summer predation by Gyrfalcon (*Falco rusticolus*) on Rock Ptarmigan (*Lagopus muta*) in northeast Iceland 1981–1997 in relation to Ptarmigan population size and expressed as predation rate. Adapted from Nielsen (1999a). The fitted trend line is a logarithmic function.

stone species as such. There are no lemmings, microtines, lagomorphs, or ungulates in this system. How the Gyrfalcon population responded to changes in Rock Ptarmigan numbers supports the conclusion that the falcon is at least one of the agents driving the ptarmigan population cycle in Iceland. Other potential influences on cyclic change in numbers are parasites (Stenkewitz et al. 2016) and nutrition (Ó. Nielsen unpubl. data). There are some discrepancies between the Iceland study and the other studies relating to how the falcons respond to changes in prey (see Tables 6 and 7 in Nielsen 1999a; and Table 10 in Nielsen 2011). The only other studies where we have an index of both ptarmigan and Gyrfalcon numbers for 10 or more years indicate a 0–1 year time-lag (Yukon; Mossop and Hayes 1994), a 1–2 year time-lag (Finnmark; Johansen and Östlyngen 2011), or a 3–5 year time-lag (Finland; Koskimies 2011) between ptarmigan and Gyrfalcon numbers. How much these differences depend on differences in population ecology or are related to methodological issues remains to be seen.

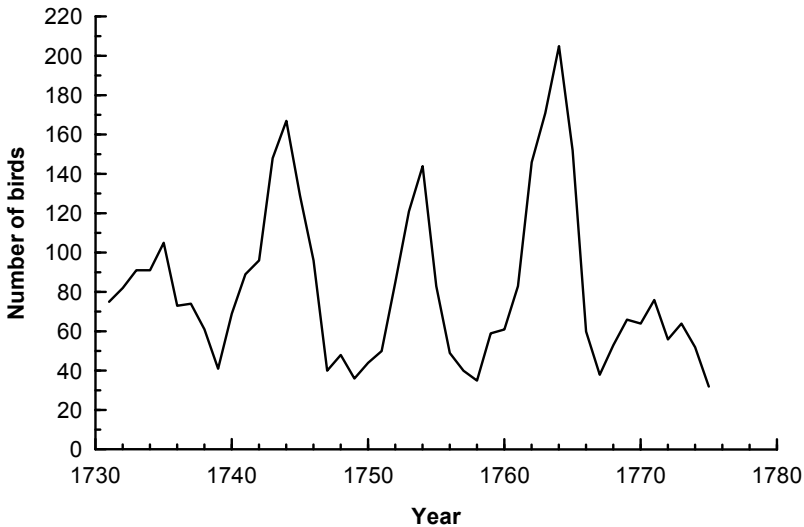
### 3.7 Life-history consequences

One would expect to see coevolution taking place for such a close-knit bond like the Gyrfalcon and ptarmigan relationship. In case of the Gyrfalcon this phenomenon should, among others, be expressed in such life-history traits as demography and timing of breeding. For the ptarmigan, the prey, one would expect to see differences among ptarmigan populations that are sympatric with Gyrfalcons as opposed to populations that are allopatric, and this should be expressed in traits such as demography and evasive abilities to reduce predation risk.

#### 3.7.1 Gyrfalcon

There is little information on the demography of the Gyrfalcon. A priori, one would expect that vital rates would show connection with ptarmigan numbers for falcon populations that base their existence solely on ptarmigan. The observed population trajectory for Gyrfalcons in Iceland suggests so (Fig. 3.6), but the demographic details have not been worked out. Another observation that has bearing on this issue is the number of grey Gyrfalcons trapped for falconry in Iceland during the 17th century (Fig. 3.9). These birds were trapped in late winter or spring and were mainly first-year birds considered part of the Iceland Gyrfalcon population. Their numbers show regular cyclical changes (Nielsen and Pétursson 1995) that probably reflect some combination of regular changes in population productivity and overwinter survival of juvenile falcons, both likely driven by an assumed ptarmigan cycle (Nielsen and Pétursson 1995).

The breeding season is an energetically demanding time for birds in general. In the case of the Gyrfalcon the female builds up reserves for egg-



**Figure 3.9** The number of grey first-year Gyrfalcons (*Falco rusticolus*) trapped for falconry in Iceland, 1731–1775. Adapted from van Oorschot (1974).

laying and incubation during the courtship period, the male provides all food well into the brood rearing period, and at the same time the adults are molting their plumage (Cramp and Simmons 1980, Booms et al. 2008). A common strategy among raptors is to time the breeding season so that it coincides with the annual peak in prey numbers (Newton 1979). The Gyrfalcon is faced with major time constraints regarding the breeding season: it is a big bird, and the breeding activities from courtship to dispersal of young take a long time—approximately 140 days—to complete. For the ptarmigan the same events from start of territoriality until the families break up in late summer take approximately 120 days, or a 20-day shorter period. Further, ptarmigan chicks are not taken in any numbers by the falcons until they are approximately four weeks or older. As a consequence the annual peak in numbers of “hunnable” ptarmigan is 4–8 weeks post-hatch or in mid and late summer. Our thesis is that Gyrfalcons time their breeding season so that their young disperse during the period when the huntable ptarmigan population is at its annual peak of numbers (see Nielsen 2003 for details). An alternative hypothesis is that Gyrfalcons time their breeding season so that the greatest demands of the nestlings on the adults—the period of most rapid growth, perhaps from 14–35 days of age—coincides with the peak in numbers of all prey or in the peak vulnerability of prey (Kim Poole, unpubl. data). In the central Canadian Arctic this peak coincides with emergence and availability of naive juvenile Arctic ground squirrels to supplement the diet and fill the gap between dimin-

ishing availability of male ptarmigan and increasing availability of females and growing ptarmigan chicks (Poole and Boag 1988).

The Gyrfalcon has been able to capitalize on adult ptarmigan for the whole breeding season by using predictable changes in behavior and vulnerability of prey. When the falcons start courtship the ptarmigan are still in winter areas (Nielsen and Cade 1990b) or moving to the breeding areas (Voronin 1987, Poole and Boag 1988). In Iceland, the behavior of the Rock Ptarmigan is changing at this season and this change affects their vulnerability. The males are not yet territorial but they are starting to show their combs and vocal aggressive encounters are frequent within the flocks. Vulnerability of the Rock Ptarmigan males peaks during the territorial period (Nielsen 1993). During this first part of the breeding season the Gyrfalcons are mainly taking Rock Ptarmigan males. In early summer after ptarmigan females have started incubation and the males have stopped displaying there is a period of low Rock Ptarmigan vulnerability, but in midsummer vulnerability increases again and now Gyrfalcon predation is directed at females leading broods (Nielsen 2003).

### 3.7.2 Ptarmigan

Many factors, environmental and biological, are important in shaping the life histories of ptarmigan (Sandercock et al. 2005, Kaler et al. 2010, Wilson and Martin 2011). It would be interesting to compare in detail the life-history traits among ptarmigan populations depending on whether they co-occur with Gyrfalcons or not. Although such study has not been done, we want to mention some issues we think are of interest. One would expect ptarmigan populations with or without Gyrfalcons as neighbors to arrange themselves on the fast-slow continuum with respect to demographic traits (Bielby et al. 2007). "Fast" populations should be characterized by a large reproductive output and low survival rates for both adult and juvenile birds. "Slow" populations should be characterized by reduced fecundity and low juvenile survival but relatively higher survival of adults (see Wilson and Martin 2011 for White-tailed Ptarmigan). Possible extremes would be ptarmigan populations exposed to Gyrfalcon predation year round, as in Iceland, which would be on the fast end of the continuum, as opposed to populations without any contact with Gyrfalcons, as in southern alpine populations, which would be on the slow end of the continuum.

We would also expect to see differences related to the evasive capabilities of ptarmigan such as wing loading, flight speed, and aerobic scope. Fat reserves are a related issue. In the harsh climate endured by ptarmigan in winter, reserves are an insurance, but they would also be a handicap where out-flying the predator is one way of escape. All studies on accumulation of fat reserves by ptarmigan in autumn have been done on birds sympatric

with Gyrfalcons (West and Meng 1968, Thomas and Popko 1981, Mortensen et al. 1985, Thomas 1986, Nielsen et al. 2013) except for Rock Ptarmigan on Svalbard (Mortensen et al. 1983), where no Gyrfalcons occur (Cramp and Simmons 1980). The median value for fat deposits of adult Rock Ptarmigan in autumn is commonly around 10 g but 250 g for adult Svalbard Rock Ptarmigan.

Another life-history trait of interest is territorial and mating behavior of Rock Ptarmigan and how sexual selection and Gyrfalcon predation seem to affect it. Rock Ptarmigan males start molting into summer plumage earlier than females and before they establish territories, but soon their molt is arrested (Pyle and James 2007). Females, on the other hand, continue the molt and are completely brown by the time they mate. In Iceland the males become territorial just after the 20th of April and they mate with the females until the third week of May (Nielsen 1993). Males look pure white throughout the territorial period and are easy to see in the now snowless landscape. The males use this noticeable plumage to advertise their ownership of the territory and do this by sitting on prominent lookout posts and performing vocal aerial displays. One consequence of this behavior is the surplus of males in the Gyrfalcons' ptarmigan catch during spring and early summer, as noted in an earlier section. This behavior and molt pattern are a good example of sexual selection, but through preferences of the females, only males that are white and defend territories can take part in mating. The ability of the male to evade Gyrfalcon predation should be the "quality check" for the female in her mate selection. After mating, the males recommence the molt, but it takes the birds some 3–4 weeks to grow brown feathers and to become fully camouflaged. A curious behavior on behalf of the ptarmigan males takes place after they have mated with the females, at which time they start taking "mud baths" and within a few days and after frequent visits to their wallows, their immaculate white plumage has turned tan and the birds are now more difficult, at least for the human being, to see (Montgomerie et al. 2001). A strange twist to this story is that if the female loses the clutch and recycles, the male will bathe in water and restore some of his earlier shine before mating again (Montgomerie et al. 2001: page 433).

If the Gyrfalcon is the agent driving the evolution of this behavior one would expect to see differences again with respect to whether the ptarmigan are sympatric with Gyrfalcons or have lived apart from Gyrfalcons for thousands of years. This question has not been studied in detail, but the asynchrony in molt between the sexes is the general rule for Rock Ptarmigan. Known exceptions are Rock Ptarmigan in Scotland and on Attu in the Aleutian Islands, where the sexes molt in synchrony, and males on Attu at least do not soil their plumage (see Montgomerie et al. 2001 and references therein). These Rock Ptarmigan populations are not sympatric with Gyrfalcons.

### 3.8 Conclusions

We have described the predator-prey relationship of a fascinating raptor, the Gyrfalcon, and equally fascinating prey, the ptarmigan, as inferred from studies in Iceland and elsewhere. The Gyrfalcon is specialized in many respects, both as to how it tackles a challenging environment at high latitudes with respect to climate and light regime, and how it hunts and uses ptarmigan as its stable diet over the annual cycle. The breeding season of the falcon is driven by events happening within the ptarmigan population. The Gyrfalcon is able to base its reproduction largely on adult ptarmigan by using changes in the vulnerability of prey related to movements from winter quarters to breeding grounds, territorial behavior of males, and behavior of females leading broods. A decline in adult ptarmigan vulnerability in midsummer is bridged by preying on alternative prey such as waterfowl, alcids, shorebirds, passerines, ground squirrels, rodents, and hares in the High Arctic. The quantity of alternative prey taken depends on ptarmigan numbers, not the number of alternative prey. This close association of predator and prey has population consequences where the falcon and the two main species of ptarmigan are sympatric throughout the annual cycle. Under such conditions, as exist in Iceland, the Gyrfalcon functions as a resident specialist predator of ptarmigan. Through its numerical and functional response, the Gyrfalcon destabilizes the dynamics of the ptarmigan population and is probably one of the drivers of the cyclic dynamics of ptarmigan (Nielsen 1999a).

Our general conclusion is that there is good knowledge of how Gyrfalcons use ptarmigan during the annual cycle. We recognize that there are knowledge gaps related to how Gyrfalcon populations respond to changes in the ptarmigan prey base (the numerical and functional responses). Addressing these gaps calls for long-term studies of both predator and prey. Such studies should address questions related to natal and breeding dispersal, migratory behavior, vital rates, and population size. Another issue not answered is whether there are populations of Gyrfalcons that base their existence on prey other than ptarmigan. There are studies suggesting this possibility from the Canadian High Arctic and Greenland, but the issue has not been settled. Further, there are many facets to the predator-prey relationship of Gyrfalcon and ptarmigan that would lend themselves to studies. Some examples include the mating system of ptarmigan and the potential influence of Gyrfalcon predation on that system, and the potential negative health factor for ptarmigan by being exposed to Gyrfalcon predation (induced stress, see Boonstra et al. 1998).

We listed some 130 different prey species taken by the Gyrfalcon (Table 3.1). Why has this potentially versatile raptor developed such a high affin-

ity for ptarmigan? We can think of several factors: 1) ptarmigan are often permanently resident, and frequently are the only prey in their size class available inland from late autumn to early spring and especially during the critical pre-laying and egg laying periods; 2) they frequently occur at high densities; 3) they are probably close to the optimum prey size for Gyrfalcons (Fig. 3.1); 4) they have large broods and as a consequence they can sustain a larger predator population than prey producing at slower rates; and 5) their vulnerability as prey for the Gyrfalcons has a predictable phenology, peaking in late winter and spring for adult males, in midsummer for adult females, and in late summer for young of the year (Nielsen and Cade 1990a).

We believe that this relationship runs deeper than suggested by the arguments listed above. One of us has collected prey remains in Iceland at well over 600 Gyrfalcon nest sites since 1981, covering the period from initiation of courtship to dispersal of young. At all these sites and regardless of the status of the Rock Ptarmigan population this grouse has been almost the only prey brought in by the male Gyrfalcon during courtship through hatching of the nestlings (March through late May). Many of these pairs have full access to alternative prey such as waterfowl and alcids as early as mid or late April, but these alternative prey are largely ignored until vulnerability of the Rock Ptarmigan diminishes in June. Even falcons nesting within a colony of 20,000–30,000 pairs of Atlantic Puffins (*Fratercula arctica*), the preferred alcid prey in Iceland, will quarter in the hills looking for ptarmigan until early June. There could be an advantage for the falcons to know the vulnerabilities and escape tactics of one kind of prey with high precision.

Maybe it is best to refer to Icelandic folklore to explain this affinity for ptarmigan (Árnason 1864: page 24). According to legend, once upon a time Mother Mary summoned all birds to her chair so they could pledge their loyalty to the Holy Mother, and did so by crossing a fire on foot. Only the ptarmigan refused to walk through the fire. This angered the Holy Mother and as a punishment she put a spell on the ptarmigan. From here on to eternity it would always be the most harmless and defenseless of birds and all the time persecuted. The Gyrfalcon, the ptarmigan's brother since the beginning of time, would be its perpetual nemesis, living by killing ptarmigan and eating the flesh. The ptarmigan should not be without salvation and the Holy Mother allowed it to change plumage according to season, be white in winter and brownish in summer in its attempt to evade its brother the falcon.

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