BIOLOGICAL TRAITS OF THE GYRFALCON (*FALCO RUSTICOLUS*) IN RELATION TO CLIMATE CHANGE

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Abstract.—Largest of the true falcons (*Falco* spp.), the Gyrfalcon (*Falco rusticolus*) is the northernmost diurnal raptor with a circumpolar breeding distribution restricted to subarctic and arctic zones between 55° and 82° N. Some Gyrfalcons migrate south into north temperate zones in winter, but others remain in northern latitudes wherever suitable prey occurs. A review of the Gyrfalcon's ecological relationships and what is known about its population history reveals some vulnerability to the potential effects of climate change on arctic environments, but also some possible mitigating adjustments. The Gyrfalcon relies on two ptarmigan species (*Lagopus* spp.) for 50-90% of its diet biomass, so it is likely that an effect of climate change on Gyrfalcons will be mediated through impacts on ptarmigan. The Gyrfalcon has trophic relations with other birds and mammals that may allow for adjustment to reduced availability of ptarmigan. The Gyrfalcon's main prey has fluctuated drastically in numbers from year to year; in peak food years a maximum number of pairs nest, but in years with low prey abundance, few breed. Under climate change the 10-year population cycles of ptarmigan and hares and the 3-4 year cycles of microtine rodents exhibit lower peaks and less regularity. Whether these population changes will persist and what they portend for predators needs study. Historically the Gyrfalcon has been the earliest nesting raptor in the Arctic. Climate change is lengthening the arctic summer, but it is unclear how Gyrfalcon breeding phenology will be influenced by this change. It could be advantageous in spring and autumn by allowing new trophic relationships. Interspecific relations with other raptors nesting in the Arctic may be influenced by climate change. The Gyrfalcon and Peregrine Falcon (*Falco peregrinus*) are potential competitors for nesting sites and food. In West Greenland, where nesting peregrines have increased dramatically in the past 50 years and Gyrfalcons have decreased, it has been suggested that the increasing number of peregrines may be forcing gyrs to abandon territories by interference competition over nest-sites or by feeding so persistently on ptarmigan during the breeding season that numbers surviving through winter are insufficient to induce gyrs to lay. The Gyrfalcon and Saker Falcon (*Falco cherrug*) are allopatric populations of closely related groups of falcons. If climate change were to alter biomes so that breeding Gyrfalcons and Saker Falcons come together, interbreeding and extensive introgression of genes likely would occur. Such hybridization might help Gyrfalcons adapt to changed ecological conditions resulting from global warming. The Gyrfalcon has a long historical association with mankind. Captive propagation now provides many Gyrfalcons for falconry. This technique could provide offspring for replenishing wild populations, should the need arise. Wild Gyrfalcons use various, manmade structures for nesting, and this habit offers a possibility to establish pairs in areas with a good food supply but no natural nest-sites. *Received 17 February 2011, accepted 31 May 2011.*

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Long admired for its variable plumage ranging from nearly white to dusky gray and for its prowess as a hunter of grouse, the Gyrfalcon (*Falco rusticolus*) is the northern-most diurnal raptor with a circumpolar breeding distribution restricted to subarctic and arctic zones from about 55ºN to 82ºN. Although some Gyrfalcons move southward into north temperate zones in winter, others, particularly adult males, remain in subarctic and low arctic regions wherever suitable prey such as ptarmigan and marine birds can be found. Adult females and juveniles wintering farther south switch from ptarmigan to waterfowl, shorebirds, corvids, pigeons, and other grouse such as Sharp-tailed (*Tympanuchus phasianellus*) and Sage Grouse (*Centrocercus urophasianus*) in North America (Cade et al. 1998, Booms et al. 2008).

Phylogenetic Relationships and Origin

The Gyrfalcon likely evolved from a Saker Falcon (*Falco cherrug*) or saker-like ancestor after tundra biotas became established following the first major glaciation at the Pliocene-Pleistocene boundary around 2 million years BP, although another idea is that this split between the two kinds of falcons did not occur until after the last glaciation around 10,000 years BP (Nittinger et al. 2005, Potapov and Sale 2005, Cade 2006). As first proposed by Johansen (1956), the Gyrfalcon may have separated from its ancestral stock at the end of the long Mindel-Riss interglacial period some 200 to 300,000 years BP, when extensive steppes connected Central Asia with arctic grasslands, allowing falcons and many other open landscape organisms to extend their ranges northward. Renewed glaciations then separated the northern proto-Gyrfalcons in a refugium from the southern sakers. Subsequent redistributions and isolations of gyr populations provided opportunities for local differentiations of white and dark birds respectively in refugia located in northwestern Greenland and Ellesmere Land and in coastal Labrador, while the ancestral gray gyrs remained in temporally shifting habitats south of the main ice masses in Eurasia and North America (Johansen 1956, Palmer 1988, Flann 2003, Cade 2006). Following the end of the last glaciations Gyrfalcons with these geographically differentiated colors have come together and interbred but have not yet achieved panmixia, thus producing the confusing mix of plumage variations we see today.

These hypotheses based on morphology and historical biogeography appear to be consistent with some of the emerging findings of molecular phylogenetics of the *Hierofalco* group of falcons, and of other avian species, but not with all of this work. For example, Wink et al. (2004) found genetic distances of 0.4% to 2.0% among the four falcon species in *Hierofalco* and estimated that this modest degree of differentiation would have occurred in a period from 200,000 to 1,000,000 years BP. They further noted that in other families of birds such small genetic differences indicate taxonomic distinction at no more than the level of subspecies. Also, estimates of species divergence times for other groups of birds, based on molecular systematics and "clocks," indicate that most recent speciation occurred from 1 to 5 million years ago (early Pleistocene to Pliocene) and that late Pleistocene isolations caused by glaciation occurred too recently to account for speciation events (Klicka and Zink 1997). These findings are in line with the view that the Gyrfalcon and saker are allopatric subspecies of one polytypic species or "allospecies" of one *Hierofalco* superspecies [see also Potapov and Sale (2005) for historical views of O. Kleinschmidt, A. Kots, and R. Meinertzhagen].

The more recent idea that the proto-Gyrfalcon became isolated from the ancestral saker only after the last major glaciation some 10,000 years BP (Potapov and Sale 2005) has been supported by recent molecular phylogenetic studies, which also emphasize the small degree of genetic differentiation between Gyrfalcons and sakers (Nittinger et al. 2005, 2007, Dawnay et al. 2007, Johnson et al. 2007). The "out-of-Africa" hypothesis of Nittinger et al. that a North African Lanner Falcon (*Falco biarmicus*) population was the ancestral source for all of the *Hierofalco* "species" seems plausible, but the further suggestion that the Gyrfalcon and Saker Falcon were independently derived from ancestral Lanner stock makes no sense from a comparison of phenotypic similarities and differences within the *Hierofalco* group or from zoogeographic considerations of their breeding ranges. These genetic studies confirm the close relatedness of the saker and Gyrfalcon with detected genetic differentiation no greater than that of subspecies in many other polytypic species of birds. The fact that none of the molecular genetic studies has so far shown a complete separation of the Saker Falcon and Gyrfalcon indicates that they should probably be considered allopatric subspecies of one polytypic species.

Whatever the real history of these phylogenetic events was, there is little doubt that the gyr has experienced repeated expansions, contractions, and fragmentations of its breeding range during the Pleistocene glaciations, and its past adaptability to survive these changes suggests that it will have considerable ability to adjust to the current climate changes that are upon us, unless they become too rapid and severe owing to anthropogenic influences. The radiocarbon dating of accumulated guano piles at Gyrfalcon eyries in West Greenland has revealed some interesting details about these changes over the past 2,500 years (Burnham et al. 2009).

RECENT CHANGES IN DISTRIBUTION

Historically recent changes in the southern limits of the Gyrfalcon's breeding range may be associated with lesser climatic events since the last major glaciation, such as the "Little Ice Age" from ca. 1300 to 1870 A.D. Two nesting pairs of Gyrfalcons were reported from the coast of southern Labrador, a "black" pair and young at the mouth of the Bras d'Or River, Quebec, at 51º28'N in 1833 (specimens collected there were the basis of Audubon's famous painting and description of the Black Gyrfalcon *Falco labradora,* Audubon 1834); a "light colored" pair also nested "for many years" in the late 1800s at Henley Harbour, 52º01'N (Townsend and Allen 1907, Todd 1963). Based on several government reports (e.g., Goudie et al. 1993), currently Gyrfalcons apparently do not breed farther south in Labrador than Harp Lake at about 55ºN inland from Hopedale. There is also a recent record of nesting on Long Island along the eastern shore of Hudson Bay at 54º53'N (Brodeur et al. 1995). The two nesting records from extreme southern Labrador may represent the last of a breeding group of Gyrfalcons that had extended their range down the Labrador coast during the Little Ice Age, when arctic conditions existed further south than they do today. None of the published maps, including the one in Booms et al. (2008), correctly depicts the southern boundary of the gyr's breeding range on the Ungava Peninsula.

Similar events may have occurred in other parts of the breeding range. On the Kamchatka Peninsula, where historical and even current records are somewhat confusing, (Dement'ev 1951, 1960, Ellis et al. 1992, Potapov and Sale 2005, Lobkov et al. 2007), local people reported Gyrfalcons nesting on coastal cliffs on the southeastern coast at the mouths of rivers at 51º09' N and 51º29'N in the late

1800s (Dybowski 1883). Today the falcons apparently do not breed regularly, if at all, south of the Kronotskiye Peninsula at ca. 54º to 55ºN and may be decreasing northward toward the Koryak District (57º42'N), where the gyr is, or has been, a relatively common nester (Lobkov et al. 2007).

Gyrfalcons also no longer nest in the Komandorskiye Islands (55ºN), where Stejneger (1885) found white birds breeding in the 1880s. There is also one outlying record of a nest found in 1924 on Matuwa Island in the Kurils at 48º04'N (Yamashina 1931, Potpov and Sale 2005). This record has been questioned, but an adult specimen exists.

Gyrfalcons in the Ural Mountains, with a north-south axis of 2,500 km reaching from low arctic to north temperate latitudes, provide another uncertain example. Sabaneev (1874) described observations (first hand and second hand) of Gyrfalcons nesting in the middle Urals at ca. 56ºN, where none occur at the present time. Dement'ev (1951) and Ellis et al. (1992) accepted these reports as valid, but they have been severely criticized by Portenko (1937) and Potapov and Sale (2005), who suggested that they were based on misidentified Saker Falcons. A key might be whether or not ptarmigan occurred in this region in sufficient abundance to support breeding Gyrfalcons. Currently, a few gyrs nest in the polar region of the northern Urals at ca. 66ºN (Potapov and Sale 2005). If the southern reports are correct, this situation would represent another major northward retraction of the breeding range since the end of the Little Ice Age.

Recently Sorokin (2009) reported Gyrfalcons nesting in 2005 and 2008 in a tall tree nest of the Imperial Eagle (*Aquila heliaca*) in a habitat of bogs and lakes with scattered islands of forest at 59ºN in the Kondo-Alymskaya Wetlands east of the Urals. This location is only about 3º of latitude north of the nearest nesting Saker Falcons.

The situation in southern and western Greenland is not well documented either. Basically all that we know is that prior to Salomonsen's monograph (1951), the Gyrfalcon was considered to be a widely distributed breeder in South Greenland and along the west coast north to Umanaq (Uummannaq) district at ca. 71ºN. Most of Salomonsen's records date prior to 1910 (Hagerup 1891, Winge 1898, and Muller 1906 all reported gyrs nesting commonly in South Greenland). Since 1981 Falk and Møller (1988, 2009) have carried out annual surveys for Peregrine Falcons (*Falco peregrinus*) in South Greenland. They have never found evidence of Gyrfalcons nesting in their study areas, which are inland where peregrines are common and ptarmigan are few. According to K. Falk (pers. comm.) the gyrs are outer coastal in distribution, and a few pairs still breed at widely scattered locations up the west coast at least as far as Nuuk (Godthab). How far north on the west coast this apparent reduction of breeders occurs is not known, but Gyrfalcons appear to be breeding less frequently than they were 30 to 40 years ago in both the Kangerlussuaq (Søndre Strømfjord) region and the Uummannaq Bay region (Burnham et al. 2005, Burnham 2007). Just when the apparent reduction in the number of Gyrfalcons in South and West Greenland began and how much it is related to natural climatic changes or to more recent anthropogenic impacts on climate and related ecological changes remains to be puzzled out, if possible, from the sparse records of the past. Again, it would be important to know what associated changes have taken place in the distribution and abundance of ptarmigan and seabirds. This whole region requires more study.

There seems to be no sign of a northward retraction of the breeding range in Norway, where nesters still occupy the historical range at least as far south as 58º–59ºN (Tømmeraas 1994). The other southern region requiring renewed investigation is northern British

Columbia, where a dozen nest sites have been recorded in alpine terrain below 60ºN (south of 58ºN in one case) in the not too distant past (Campbell et al. 1990).

ADAPTATIONS TO A COLD CLIMATE

The Gyrfalcon is the largest of the true falcons (fat-free males typically range from 1,000 to 1,400 g, females from 1,250 to 2,000 g), and this large body size is no doubt advantageous for existence in a cold climate owing to the reduced heat loss related to the lesser surface to volume ratio of its body compared to that of smaller birds. It also has dense downy plumage with large, fluffy aftershafts on the contour feathers and partially feathered tarsometatarsi, additional features that confer bioenergetic and thermoregulatory advantages for existence in the cold. Under good feeding conditions, the gyr can accumulate 200 to 300 or more grams of body fat, and it can temporarily store that much food in its crop (Cade 1999). These energy stores permit the gyr to seek shelter from severe storms and high winds and to remain inactive for several days on end without metabolizing any of its muscle mass for energy. Although no physiological study has been performed, observations on the lethargic behavior of captive birds (Palmer 1988) under certain conditions suggest that the Gyrfalcon may also drop its body temperature a few degrees centigrade and reduce its metabolic rate during these periods when it cannot hunt for food.

FOOD AND TROPHIC RELATIONS

The gyr feeds mainly on ptarmigan (*Lagopus* spp), often 50 to 90% of annual diet, and the breeding and wintering distributions of the Gyrfalcon parallel very closely those of the Rock Ptarmigan (*Lagopus muta*) and the Willow Ptarmigan (*Lagopus lagopus*). This close trophic relationship has evidently existed throughout the Pleistocene Epoch. It seems likely that any major impact of climate change on gyr populations will be mediated through impacts on ptarmigan distribution and abundance. Even so, gyrs do use alternative prey in some situations—notably seabirds (alcids and gulls), waterfowl and shorebirds, passerines such as the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*), hares (*Lepus* spp) and Ground Squirrels (*Spermophilus undulatus*), and lemmings and voles during peak years. Also, the avian predators of microtine rodents such as the Long-tailed Jaeger (*Stercorarius longicaudus*), Parasitic Jaeger (*Stercorarius parasiticus*), Short-eared Owl (*Asio flammeus*), and even the Northern Harrier (*Circus cyaneus*) can be significant in the diet in some years (Cade 1960, Cade et al. 1998, Potapov and Sale 2005, Booms et al. 2008).

Under climate change some of these species could become important substitutes, if ptarmigan populations undergo serious declines or shifts in distribution and abundance away from historical falcon nesting habitats. For example, ground squirrels might start emerging earlier in spring and increase in number as permafrost melts and drier, ice-free soils become more available to burrowing rodents. These conditions are also likely to favor the Red-backed Vole (*Myodes rutilus*) and the Singing Vole (*Microtus miurus*), but the wetland Brown Lemming (*Lemmus trimucronatus*) and Tundra Vole (*Microtus oeconomus*) can be expected to decline. Likewise, increase in shrubby vegetation (especially willows) and extension of spruce trees northward could promote permanent establishment of the Snowshoe Hare (*Lepus americana*) in the Low Arctic of North America. An instance of the invasion of this hare into the Colville River valley of Arctic Alaska occurred in the 1990s (T. Swem pers. comm.). Changes in the distribution and abundance of seabirds, waterfowl and shorebirds, and passerines—as well as ptarmigan—can all be expected under a continuing regime of global warming, sometimes to the benefit of the Gyrfalcon, sometimes not (Hamer 2010).

BREEDING BIOLOGY

Historically the gyr has been the earliest breeding raptor in the Arctic, laying in April (even late March) to mid-May, depending on latitude, and close in timing to the Common Raven (*Corvus corax*), another early breeder, the old stick nests of which often provide gyrs with needed nesting substrates. Early breeding seems necessitated in part because the gyr has a long reproductive cycle of ca. 160–180 days from establishment of nesting territory to independence of fledged young in mid- to late August, shortly before winter begins. Breeding also seems to be timed so that nestlings fledge during the period of peak availability of young, inexperienced prey, especially ptarmigan (see Potapov and Sale 2005, Figure 7.1). It is unclear just how climate change, especially warming, may change the breeding phenology of the gyr relative to that of its prey, but contrary to expectation, Gyrfalcons in Yukon Territory are now breeding later than they used to do (see D. Mossop, this conference).

Gyrfalcons usually nest on cliffs in a location well protected from weather, often on a high wall of rock but also on some remarkably low rocks only a few meters above the ground. In some areas, especially in Eurasia, they also use old stick nests of other birds in trees, particularly those of Common Ravens but also eagles, Rough-legged Hawks (*Buteo lagopus*), and a few other species. Some cliff sites can only be occupied when stick nests are present. As old stick nests are ephemeral, gyrs can only occupy tree nesting sites and some cliffs when a suitable stick nest is present, and this fact probably accounts for the many one-time or two-time nest occupancies that characterize the Gyrfalcon, as compared to the peregrine.

In many parts of the range, nest sites appear to set an upper limit to nesting population size, but in years of low ptarmigan numbers breeding pairs of falcons are reduced below the number of available nest sites, because the Gyrfalcon has a limited ability to switch to alternate prey, particularly early in the breeding cycle when females must build up their nutritional reserves for reproduction (see N. Barichello, this conference). On the other hand, in years of exceptional abundance of ptarmigan, some pairs of gyrs will occupy marginal nest-sites that in most years would not be used. Such a situation occurred on the Colville River in arctic Alaska in1990 when 26 pairs nested in a region that usually holds only eight to 14 pairs (T. Swem pers. comm.).

In most gyr populations the establishment of breeding pairs and the onset of laying are closely tied to the late winter and early spring abundance of ptarmigan. This dependence appears to apply even to pairs that switch later in the breeding cycle to feeding on seabirds or on waterfowl and shorebirds. Gyrfalcons nesting in the Thule region of northwestern Greenland begin laying in May at about the time Dovekies (*Alle alle*) first arrive on their nesting cliffs. Several authors have noted this correspondence in the time falcons lay and the arrival of seabirds (Dement'ev and Gortchakovskaya 1945, Salomonsen 1951, Cade et al. 1998, Potapov and Sale 2005, Burnham 2007), but the critical point is that the female gyr has probably spent a month or two on her nesting territory building her energy reserves for reproduction prior to the arrival of the seabirds, which are late nesters. Ptarmigan and hares are about the only prey available at that time. In the autumn during their dispersal and migration from the breeding grounds, young Gyrfalcons depend mainly on juvenile ptarmigan, microtine rodents, and juvenile passerine birds for food (Cade et al. 1998, Booms et al. 2008).

Another aspect of breeding is that like most avian predators in the Arctic (jaegers, owls, and diurnal raptors with the notable exception of the Peregrine Falcon), the Gyrfalcon's ptarmigan prey base fluctuates or cycles drastically in numbers from year to year, so that in peak periods of food abundance, a maximum number of pairs attempt to breed (but success still depends mainly on good weather); whereas, in years of low prey abundance fewer pairs attempt to breed. Under climate change the 10-year population cycles of ptarmigan and hares and the 3- to 4-year cycles of microtine rodents appear to be damping with lower peaks and less regularity between high and low years (e.g., Gilg et al. this conference). Whether these population changes will persist and what they portend for predators needs more study, but it seems clear that until now the Gyrfalcon has successfully adjusted to the cyclic and irregular fluctuations in density of its principal prey by capitalizing on the occasional peak years of reproduction to counter the low productivity of sparser years.

INTERSPECIFIC RELATIONS WITH OTHER RAPTORS

Among the diurnal raptors regularly breeding in the Arctic, only the Gyrfalcon and Rough-legged Hawk are arctic specialists; the peregrine, Golden Eagle (*Aquila chrysaetos*), and White-tailed Sea Eagle (*Haliaeetus albicilla*) (also the raven) are generalists with extensive breeding distributions in other regions. The latter are likely to be winners as climate change modifies the ecological conditions of the Arctic, while the former are more likely to be losers (Hamer 2010).

The peregrine and Gyrfalcon are potential competitors for nesting sites and for food (Salomonsen 1951, Cade 1960). In arctic Alaska where gyrs and peregrines often nest in the same localities and sometimes together on the same cliffs, it appeared that the gyr dominated the peregrine in interactions over nest-sites because of its larger size and earlier breeding season (Cade 1960, White and Cade 1971). In West Greenland, where nesting peregrines have increased dramatically during the past 50 years and Gyrfalcons have decreased or disappeared progressively from south to north, it has been suggested that the increasing number of Peregrine Falcons may be forcing gyrs to abandon territories by interference competition over nest-sites or by feeding so persistently on ptarmigan during the breeding season that their numbers surviving to early spring of the following year are below the level that induces gyrs to begin laying (Burnham 2007). The less diverse and abundant prey base in Greenland compared to northern Alaska could be a factor tipping the competitive advantage to the Peregrine Falcon in Greenland; whereas, the richer prey base in Alaska may mitigate competition for food between these two species, and an abundance of nest-sites reduces competition for suitable places to breed.

Alternatively, the gyrs may be abandoning nesting sites for reasons other than competition, such as overall change in the distribution and abundance of prey species, and then the peregrines take over the abandoned nest-sites. Nelson (1969) reported an example of such a situation in which Prairie Falcons (*Falco mexicanus*) took over the abandoned eyries of Peregrine Falcons during a prolonged period of drought and DDT use in the Pacific Northwest of North America in the 1940s to 1960s.

As previously discussed, the Gyrfalcon and Saker Falcon are disjunct, allopatric species or subspecies of two closely related groups of falcons. In captivity their gametes are fully compatible, producing not only F_1 hybrids that produce fertile offspring by backcrossing with either parental species but also fertile hybrid to hybrid crossings through successive generations (Heidenreich et al. 1993, M. Heidenreich pers. comm., N. Fox and associates unpublished data). If climate change should alter biomes in such a way that breeding populations of Gyrfalcons and Saker Falcons eventually come together, there is little doubt that interbreeding would occur between the two with extensive introgression of genes. Such hybridization might actually help Gyrfalcons adapt to the changing ecological conditions brought on by global warming. It is likely that hybridization between gyrs and sakers has already occurred one or more times during the Pleistocene, as evidenced by the intermediate characteristics of the "Altai Falcon" in central Asia (see Potapov and Sale 2005 for an extended discussion; also, Eastham 2000).

RELATIONS WITH HUMANITY

Like the Peregrine Falcon, the Gyrfalcon has had a long history of association with mankind in the sport of falconry (Dement'ev 1960, Potapov and Sale 2005). It has always been the most prized of all the hunting falcons used in falconry because of its large size and rarity—and great beauty—and gyrs were often exchanged as gifts among potentates. The species is still sought after today, and both legal and illegal trade occur, mainly to the Middle East. Captive propagation now provides large numbers of gyrs for falconry, a proven technique that could also be used for re-establishing wild populations, should the need arise.

A problem that needs international consideration is that the number of wild founders of the worldwide captive breeding stock was quite small, almost certainly fewer than 40 birds, some of which were closely related to each other and perhaps only half of which were prolific breeders. This situation has led to much inbreeding, especially within the breeding stock of individual propagators, despite the several thousand falcons that have been commercially produced for falconry in the past 40 years. A reduction in body size and egg size has become evident in the more recent generations of falcons; reproductive problems and other signs of inbreeding depression are also appearing. Line breeding for specific colors (extreme white, extreme dark) and large body size has exacerbated inbreeding. Unfortunately, there has been limited exchange of unrelated individuals among propagators, and some commercial breeders cannot be relied upon to maintain the protocols and studbook data required for proper genetic management of their breeding stock. Consideration should be given to the acquisition of new, wild breeding stock to counter inbreeding problems, particularly in the case of any conservation breeding projects that may develop for future reintroduction and restocking purposes.

Furthermore, despite the CITES treaty, which provides a framework for international trade in wildlife, inconsistencies among nations and burdensome regulations in various countries discourage and in some cases prohibit trade. Government has the responsibility to help maintain the health and fitness of captive Gyrfalcon populations to insure that captive bred falcons remain a viable alternative to wild birds, both for the sport of falconry and for conservation. Current policies and rules favor the commercial propagators and make it extremely difficult for private, nonprofit breeders and scientists to export and import birds needed to maintain the genetic viability of their breeding stock.

Wild Gyrfalcons are also known to use various manmade structures for nesting, and this habit offers a possibility to establish nesting pairs in areas with a good food supply but no natural nest-sites, as is currently being done for the Saker Falcon in Mongolia (see A. Dixon this conference; also A. Østlyngen and K. Johansen this conference; V. Morozov this conference). Currently many such areas exist throughout the circumpolar arctic regions, and more may be created as global warming progresses.

CONCLUSION

It seems likely that the aspect of the Gyrfalcon's life history that will be most vulnerable to the impacts of climate change is its dependence on ptarmigan as its main source of food in the early stages of the annual breeding cycle before eggs are laid and young hatch. Even though gyr populations in several kinds of situations can shift effectively to feeding on seabirds, waterfowl and shorebirds, or on other species of birds and mammals after their eggs hatch, there appears to be no situation in which they can breed successfully in the absence of substantial numbers of ptarmigan at the time females are storing energy for egg production. Arctic hares, or possibly lemmings, under some circumstances where they occur in sufficient numbers, might be an adequate substitute for ptarmigan, or even seabirds wintering on polynyas within the foraging range of nesting gyrs; but I know of no case in which such situations have actually been observed to occur. The Gyrfalcons nesting on Ellesmere Island and surrounding islands should be investigated from this standpoint in the early season (see Cade and Bird 2011, Muir and Bird 1984).

A longer and warmer arctic summer might offer Gyrfalcons some opportunities to adjust their annual cycle to new sources of food during their pre-laying period. The falcons might adjust by delaying their reproductive cycle until after adequate prey arrive on their territories, an adjustment made possible by the later fall freeze-up, allowing time to complete their long breeding cycle. Conversely, prey such as seabirds, waterfowl, shorebirds, even ground squirrels, may start appearing on the scene much earlier than previously, providing a supplement to whatever ptarmigan are still available. A wintertime shortage of ptarmigan in the Arctic and Subarctic also may force more Gyrfalcons to migrate into temperate zones during winter. In other words, the Gyrfalcon may have to become more like the arctic-breeding Peregrine Falcon in the characteristics of its annual cycle—breeding later in relation to the arrival of suitable prey, feeding on a wider assortment of prey species, and migrating farther away from its breeding territories in winter. Such changes might, however, lead to increased competition between these two species of falcons. These are all intriguing possibilities that will need to be anticipated and monitored carefully in the coming decades.

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