

CONFERENCE SUMMARY

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DURING THIS CONFERENCE we have been treated to a mass of new information from around the Northern Hemisphere, not just on tundra-dwelling Gyrfalcons and Ptarmigans, but also on seabirds and other relevant wildlife, and on the arctic environment in general. It is not easy to summarize all this information, so I will instead pick out a few salient impressions for emphasis.

CLIMATE CHANGE

I think we can all accept that the Arctic is warming, that this trend is largely or entirely human driven, and that it will continue into the foreseeable future whatever the trends in greenhouse gas emissions. Effects so far recorded fit the earlier prediction from climate models that warming will be greatest at the highest latitudes. During the 20th Century, mean arctic temperatures, averaged across all regions, rose by 2–3 °C, compared to an average of 0.6 °C for the earth as a whole. Much of this change occurred after 1980. In association with this warming trend, the area of sea-ice is shrinking year by year, glaciers are retreating,

spring is coming earlier, and the general distribution patterns and phenology of plant and animal species are in process of change. In this conference we have heard how tree-lines and shrub-lines are advancing northward, and how willow patches are expanding in many places but not everywhere. As the arctic tundra already extends northward to the Arctic Ocean, occupying in most places all the land available, over time the total amount of tundra habitat is bound to shrink, despite substantial likely expansions in Greenland and elsewhere, as ice retreats. Dominique Bachelet predicted a loss of up to 90% of existing tundra in Alaska by 2100. So overall, our star species—Gyrfalcon and ptarmigan—could decline substantially in the long term.

Two studies examined likely changes in the distributions of the Gyrfalcon, Willow Ptarmigan, and Rock Ptarmigan, based on their current ‘climatic envelopes.’ The method entails calculating the range of climatic conditions (based on key climatic variables) in which the species now live, and then, on the basis of various climatic models, finding where the same range of

conditions is likely to be found at some future date (say 2100 AD). The study by Rhys Green and Brian Huntley dealt with the global distributions of all three species, while the study by Travis Booms and colleagues dealt with their Alaskan distributions only, but incorporated additional information on geology and elevation. Using different climate models, both studies predicted substantial declines in the ranges of all three species, and Booms et al. additionally predicted greater fragmentation of ranges and reduced overlap between the ranges of Gyrfalcons and ptarmigan (an aspect not presented by Green and Huntley). In the Green-Huntley study, areas with suitable climate for Gyrfalcons and ptarmigan were projected to be lower in extent in the late 21st Century than at any of the various times they considered in the last 120,000 years.

To me one of the most worrying findings of recent years has been a breakdown in several regions of the long-standing cyclic fluctuations of various arctic herbivores, including rodents, hares, and ptarmigan. In all these species, cycles of abundance tend to be more marked, with wider amplitude, from south to north across the range. Disruption or stopping of cycles has been noticed in Snowshoe Hares over much of northern North America, in lemmings and other rodents on east Greenland (Olivier Gilg at this meeting), northern Europe and Russia, and in ptarmigan in southern Yukon (Dave Mossop at this meeting) and elsewhere. For predators that depend on peaks in these prey species to achieve sufficient reproduction of their own, this breakdown can only be bad news. Olivier Gilg mentioned that in east Greenland Long-tailed Jaegers had returned to their territories for ten successive springs but had not bred in any of those years, owing to the lack of a peak in lemming abundance. I shall return to this point below.

In addition to climate, other likely high latitude changes in the Arctic mentioned during our meeting included: more ‘opening up’ of the

Arctic in association with greater oil and mineral exploration and extraction work, greater pollution in association with these and other activities, more shipping and pollution in the Arctic Ocean, increasing human populations, changing life-styles and behavior of native people, more hunting of ptarmigan and greater illegal take of Gyrfalcons, the latter especially in Russia and Siberia.

PHYLOGENETIC STRUCTURE

The regional variations in coloration within the circumpolar distribution of the Gyrfalcon have been well-described in the past, and taxonomists have used this variation to delineate a number of subspecies, none of which are given much recognition currently. Recent molecular work by Jeff Johnson and others has confirmed that the overall population is indeed genetically structured and that the island-populations of Greenland and Iceland are each fairly well separated from the rest. Provisionally, it seems that the genetic sub-structuring (based on mtDNA) does not match the geographic variation in morphology, but more material is needed, especially from Russia and Siberia.

It seems from DNA analyses that Gyrfalcons and Saker Falcons are very closely related, and shared a recent ancestor. As Tom Cade reminded us, the two species appear to intergrade in at least one area (the Altai), and in captivity they interbreed readily. Hybrids of both sexes are fertile when paired to one another, and when back-crossed to either parent species. It is therefore not impossible that the two species, currently separated by the boreal forest (with the Gyrfalcon to the north and the Saker Falcon to the south), could merge again if this forest barrier was reduced by climate or other human-induced change. Eugene Potopov mentioned one region where the two species were nesting only 120 km apart, but he did not know whether this situation was new or of long-standing.

RELATIONSHIP BETWEEN GYRFALCONS AND PTARMIGAN

My impression, from what we have heard at this conference, is that the Gyrfalcon is best considered as a generalist predator which, through dint of circumstance, has to specialize. Over most of its current range, for more than half of each year, it finds itself dependent on one or two species of ptarmigan—the only prey species consistently available. This dependence on ptarmigan clearly puts constraints on the falcon, and to a large extent underpins its whole ecology and population dynamics. Several speakers stressed the early breeding, with pairs on site in January-February (at least in the southern parts of the range), when the sun barely rises above the horizon and temperatures are extremely low. The eggs are laid mainly in April, a time in late winter when food supplies reach their lowest level of the year, when days are still short and cold, when mammals are still under ground or under snow, and well before any migrant birds suitable as prey have returned to inland areas. Several speakers stressed the dependence of annual reproduction on ptarmigan numbers at this time of year (in turn dependent on ptarmigan breeding success in the previous year). In the Yukon, Gyrfalcon productivity varied up to 13-fold between years, in association with late winter ptarmigan abundance (Norman Barichello and Dave Mossop). In addition, the proportion of first-year birds in the late winter ptarmigan population (which was correlated with abundance) had a positive effect on Gyrfalcon reproduction, beyond the effect of abundance alone. This may have been because first-year birds are easier to catch. Similar, but less extreme, relationships between Gyrfalcon reproduction and late-winter ptarmigan abundance also emerged from studies in Iceland (Oli Nielsen), Alaska (Brian McCaffery), Finland (Pertti Koskimies), and elsewhere. Ptarmigan availability mainly affected the proportion of Gyrfalcon pairs which laid each year, and the proportion of pairs which went on to incubate those eggs (rather than deserting

them), but it also affected the date of egg-laying and the clutch-size. Later in the season, as young mammals emerged, and migrant birds arrived and produced young, feeding conditions rapidly improved. Over the period April to August, according to Eugene Potopov, the number of prey species recorded in the Gyrfalcon diet increased from 1–2 to more than 40. It seems, then, that productivity is limited primarily by food-supply (= ptarmigan abundance) in late winter, and that any additional variation in productivity added later in the season is more likely due to weather conditions than to prey abundance.

Of course some other meat-eating birds also lay their eggs early in the year. In the Arctic, both Golden Eagles and Ravens lay early, as do these and other raptors further south. But all these other species take a wider range of prey, and all eat carrion, which is often abundant in late winter. The greater ability of Golden Eagles to take large hares (as well as ptarmigan) gives them an advantage over Gyrfalcons, and the ability of Ravens to scavenge from the kills of other avian and mammalian predators increases the options available to them. None of these other species seems quite so constrained and dependent on ptarmigan as do Gyrfalcons.

Many presenters spoke of the cycles in ptarmigan numbers, with peaks occurring at intervals of 3–4 years in northern Europe and Russia (Pertti Koskimies), 5–7 years in west Yakutia, 8–10 years in east Yakutia (Arkady Isaev), Kamchatka (Evgeny Lobkov) and North America (Kathy Martin), and 11 years in Iceland (Oli Nielsen). In most regions, these cycles seem tied to similar cycles in mammalian herbivores, whether small rodents or hares, but this is not the case in Iceland where no such mammals occur but ptarmigan numbers still fluctuate in cyclic fashion. Reproductive output in Gyrfalcons fluctuates from year to year simultaneously with change in ptarmigan numbers, with peak production in peak ptarmigan years. However, individual Gyrfal-

cons do not normally breed until they are three (range 2–4) years old, so peak production in one year is followed by peak recruitment three years later. Presumably for this reason, the territorial population of Gyrfalcons tracks the ptarmigan cycle, but with an approximate three-year lag. This was shown most clearly in the studies of Dave Mossop in Canada and Oli Nielsen in Iceland. In northern Europe, with a 3–4 year ptarmigan cycle, young falcons produced in one peak ptarmigan year should be recruited three years later in the next peak ptarmigan year.

To me it was surprising that, in a large long-lived bird like a Gyrfalcon, breeding numbers should be so dependent—on a year-to-year basis—on previous breeding success. This is the sort of relationship previously shown in short-lived high-reproducing birds, such as game birds, ducks, and passerines. This observation made me wonder how high Gyrfalcon mortality might be at times of ptarmigan lows.

We were given further indications of the importance of ptarmigan to Gyrfalcons. Vladimir Morozov described a region in the Polar Ural Mountains and Yamal Peninsula in which ptarmigan remained at an extremely low level for six consecutive years during which Gyrfalcons apparently disappeared completely, only to start re-colonizing in more recent years. Ivan Pokrovsky described areas where Gyrfalcons do not extend to the northern limit of the tundra, and where Peregrines become the most northerly breeding falcon species. As a further thought, Gyrfalcons occupy only part of the range of ptarmigan, being wholly absent from southern areas. Could this be because the amplitude of ptarmigan cycles is too low in southern areas to provide the high peaks on which good Gyrfalcon breeding depends? In this case, the absence of Gyrfalcons from such southern areas would not be due to the absence of ptarmigan prey, but to the wrong prey dynamic; but this is, of course, largely unfounded speculation in need of further study.

One other point mentioned about Gyrfalcon breeding was the variation in productivity between nesting territories. As in some other raptors, it was noticed that, over a period of years, those Gyrfalcon territories that are most often occupied show the highest annual breeding success, whereas less frequently occupied territories are less productive. This point was made most strongly by Ulla Falkdalen in mid-Sweden, where over a period of years 14% of all territories produced more than half of all young. Another finding for Gyrfalcons, common to some other raptors, was the tendency for pairs that lay early in the season to raise most young, and later ones fewer (Norman Barichello and Dave Mossop).

NEST SITES

In general, in the absence of human intervention, raptor breeding densities could be limited by food or nest-sites, whichever resource is in shortest supply in particular areas. Gyrfalcons nest on cliffs or trees, favoring old stick nests of other birds (including White-tailed Eagle, Golden Eagle, Rough-legged Hawk, Raven and others). In North America and elsewhere, cliffs are the most often used sites, but over large parts of the taiga region of Eurasia trees are the most often used. Not surprisingly, there are no records of tree-nests from Iceland and Greenland, although both had historical birch forests that might have been suitable. Gyrfalcons may also use man-made structures, including artificial nest-sites placed on cliffs or in trees. We were told that, after recently-recorded patterns of freeze, thaw, and re-freeze, Gyrfalcons may sometimes have difficulty in clearing snow off some old nests, that unstable stick nests on cliffs occasionally collapse, and that from small crow nests in trees, young may fall out and die (Svetlana Mechnikova). Among tree nests, a significant correlation emerged between nest size and final brood size.

While over much of the range, Gyrfalcon breeding densities may be limited by ptarmi-

gan abundance, they are unable to breed in some areas through lack of nest-sites, whether cliffs, trees or man-made structures. In various areas, provision of artificial structures has led to increased local nesting densities or extended the breeding into areas where it was not previously possible (Vladimir Morozov, Arve Østlyngen, Oleg Mineev). No doubt, if it was felt desirable to increase Gyrfalcon breeding numbers or distribution, nest sites could be provided on a larger scale, as described for the Saker Falcon in Mongolia by Andrew Dixon.

Like some other large raptors, Gyrfalcons use particular cliff sites over long periods, but particular pairs may alternate between two or more sites in the same vicinity (Travis Booms et al., Peter Bente). Carbon-dating of ancient fecal matter taken from existing nest structures in northwest Greenland indicated continual use over periods exceeding 2,000 years, from the time such cliffs were first exposed by glacial retreat (Kurt Burnham).

MOVEMENTS

The very few ring recoveries available for Gyrfalcons tell us little of use about their movements. The three radio-tracking studies reported at this conference from Alaska (Carol McIntyre), Greenland (Kurt Burnham) and Sweden (Ulla Falkdalen) provide the first useful data on movements. They all show that young Gyrfalcons disperse in various directions from their nest areas, but the longer movements tend to be southward, or at least to lower latitudes. Most individuals extend up to a few hundred kilometers, but some up to a few thousand kilometers, as recorded in Alaska and Greenland. The Greenland work also revealed the extent to which some Gyrfalcons forage at sea in winter, remaining at sea for weeks at a time. These birds are presumed to sit on ice, and hunt seabirds, such as auks and ducks. This behavior presumably enables them to break away from ptarmigan-dependence in winter, but it is not an option available to much of the total population. These studies also

revealed the huge home ranges of individuals in winter (up to many thousands of square kilometers), the frequent movements made in winter, and the variability of behavior between individuals.

One might wonder why Gyrfalcons do not leave the Arctic to winter in more temperate latitudes where a wider range of prey species is available. For adults (especially males), the answer seems to be that they have to guard their precious nest sites in winter (where they can be seen from at least January on) and be there for egg-laying in April. Juveniles have no such constraints, but only a few reach the temperate zone in winter. For all we know, they may not survive well there.

INTERACTIONS WITH OTHER SPECIES

Apart from their heavy dependence on ptarmigan as prey, Gyrfalcons over much of their range clearly depend on other species to provide nest-sites, especially Ravens, hawks and eagles. Some other raptors, notably Peregrines and Golden Eagles, also take ptarmigan, so in theory could compete for them with Gyrfalcons, as could human hunters. Burnham stressed the potential for competition for nest sites between Gyrfalcons and Peregrines, which in Greenland are increasingly spreading north into Gyrfalcon range. The Gyrfalcons are larger, and start nesting earlier, but later-arriving Peregrines settling nearby constantly harass Gyrfalcons, and could kill their young. Several speakers from Russia and Siberia stressed the rapidly increasing brood robbing by people, an activity fuelled by the growing market for Gyrfalcons in the Middle East (Eugene Potapov, Ivan Pokrovsky and Evgeny Lobkov). A recent decline in breeding numbers in Kamchatka was attributed to such over-harvesting (Evgeny Lobkov).

In addition to these adverse developments, some trends may have positive effects on Gyrfalcons. Two mentioned in this conference include the reduced fur trapping in Rus-

sia and Siberia (which reduces the numbers of falcons killed incidentally in traps), and the earlier break-up of sea ice, which allows seabirds to reach far northern regions earlier than in the past (giving an earlier-available additional food source for Gyrfalcons living near the coast).

PRIORITIES FOR FUTURE WORK

During the conference, up-to-date population estimates were given for several regions, and it might be possible to pull together these estimates into an overall estimate for the global population. But given the threat of climate warming, already well advanced in the Arctic, is there any evidence that Gyrfalcons are retreating or declining in the southern parts of their range? Tom Cade mentioned to me that the site in Labrador where Audubon shot the type specimen of *Falco labradora* in the 19th Century was now about 3° of latitude south of the southern edge of the current breeding range. Elsewhere in southern parts of the range, likely declines have been detected in the southern Yukon (Dave Mossop), in western Greenland around Kangerlussuaq (Kurt Burnham), and in Kamchatka (Evgeny Lobkov). No speaker mentioned declines from areas further north in the range (other than through poaching in parts of Russia and Siberia): in Finnmark numbers were little different in recent years from those recorded 150 years ago (Kenneth Johansen), and in northern Alaska from those recorded 30–50 years ago (Ted Swem). Similarly, several speakers mentioned declines in Willow Ptarmigan in southern parts of their range in North America (Kathy Martin) and in Russia-Siberia (Eugene Potopov), or White-tailed Ptarmigan moving upslope in Glacier National Park, Montana (David Benson).

During the conference more than a dozen areas from across the Arctic were mentioned from which multi-year studies of Gyrfalcons had

been made, so for at least these areas, we have a good basis of quantitative information against which to measure change. It is desirable, therefore, that at least some of these studies be continued, giving priority to those that can be accessed in late winter (say March-April) around the time of egg laying, when important things happen, and where ptarmigan can be counted with reasonable accuracy. But are there also other areas which should be looked at: for example, where Gyrfalcons might differ in ecology or depend on different prey?

Ideally, future studies should be aimed not just at monitoring numbers and nest success, but at gaining more understanding of the relationships between Gyrfalcons, ptarmigan, vegetation, and snow cover, and also the links between ptarmigan, mammalian herbivores, vegetation and snow cover. It would also be useful to have more studies of mortality rates in adults and immatures, and of dispersal. Does the figure of 20% adult mortality provided by Travis Booms et al. from Alaska hold more widely, and throughout the ptarmigan cycle, or are there periods of heavier mortality at times of ptarmigan lows? Newly-developed techniques for measuring survival and movements over large areas, such as the DNA-fingerprinting of individuals from their feathers described by Travis Booms, have great potential to add value to future monitoring studies. Clearly, there is more scope for demographic studies of the type reported for Arctic-nesting Peregrines by Alistair Franke and his colleagues, and it would help in future Gyrfalcon studies if methods were standardized to a greater extent than at present.

In summary, we can say that, while Gyrfalcons may be under threat from climate change and other developments, they do not yet seem to be in catastrophic decline, being still found over huge areas of the arctic tundra of North America, and of the tundra and taiga of Eurasia.