Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere

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Abstract

This paper reviews factors affecting site selection amongst waterfowl (Anatidae) during the flightless remigial moult, emphasising the roles of predation and food supply (especially protein and energy). The current literature suggests survival during flightless moult is at least as high as at other times of the annual cycle, but documented cases of predation of flightless waterfowl under particular conditions lead us to infer that habitat selection is generally highly effective in mitigating or avoiding predation. High energetic costs of feather replacement and specific amino-acid requirements for their construction imply adoption of special energetic and nutritional strategies at a time when flightlessness limits movements. Some waterfowl meet their energy needs from endogenous stores accumulated prior to remigial moult, others rely on exogenous supply, but this varies with species, age, reproductive status and site. Limited evidence suggests feather proteins are derived from endogenous and exogenous sources which may affect site selection. Remigial moult does not occur independently of other annual cycle events and is affected by reproductive investment and success. Hence, moult strategies are affected by age, sex and reproductive history, and may be influenced by the need to attain a certain internal state for the next stage in the annual cycle (*e.g.* autumn migration). We know little about habitat selection during moult and urge more research of this poorly known part of the annual cycle, with particular emphasis on identifying key concentrations and habitats for specific flyway populations and the effects of disturbance upon these. This knowledge will better inform conservation actions and management actions concerning waterfowl during moult and the habitats that they exploit.

Key words: Anatidae, energy balance, feather synthesis, moult, predation, protein, survival.

Normally annual replacement of avian remiges (hereafter flight feathers) is essential, because damage, abrasion and exposure to ultra-violet light degrade such tissues (Stresemann & Stresemann 1966; Bergman 1982). Allometric relationships underlying the production of feather tissues proportionally prolong replacement of flight feathers in larger (> 300 g) birds (Rohwer *et al.* 2009). For this reason, large bird species extend flight feather moult over two or more seasons (*e.g.* Bridge 2007) or, as is the case amongst birds that do not rely on the powers of flight for feeding, undergo a simultaneous moult of all flight feathers that renders them flightless temporarily, including species of the Alcidae, Anatidae, Anhingidae, Bucerotidae, Gavidae, Gruidae, Heliornithidae, Jacanidae, Pelecanoididae, Phoenicopteridae, Podicipedidae, Rallidae and Scolopacidae (Stresemann & Stresemann 1966; Marks 1993). With the notable exception of the Bucerotidae, where breeding females undergo simultaneous moult whilst sealed inside nest cavities by males (Stonor 1937; Moreau 1937), the common feature of all these avian families is their occupancy of aquatic or marine habitats. Indeed, of the avian families that forage primarily on or under water throughout the annual cycle (*i.e.* excluding seabirds that forage on land or on the wing; Fregatidae, Laridae, Procellariiformes and Sternidae), members of the Anatidae, Alcidae, Gavidae, Pelecanoididae and Podicipedidae replace their flight feathers synchronously whilst in wetlands, most often on water. To minimise the omnipresent mortality risk posed by aquatic and aerial predators throughout the annual cycle, these species exploit aquatic systems that expose them to relatively low predation risk within and outside the flightless remigial moult period. Furthermore, the moult of males of several species of waterfowl from a bright breeding plumage (the alternate plumage according to Palmer 1972 and Weller 1980, basic according to Pyle 2005) to a cryptic eclipse plumage prior to the wing feather moult (the basic plumage according to Palmer 1972 and Weller 1980, the alternate according to Pyle 2005) is likely, at least in part, an adaptation to reduce conspicuousness during this highly vulnerable period. Loss of the powers of flight also reduces foraging opportunities, so a likely determinant of habitat selection during remigial moult is the need to derive sufficient energy and nutrients to satisfy maintenance requirements and supplementary needs of feather replacement (Hanson 1962; Hohman *et al.* 1992).

For example, the massive aggregations of Eared Grebes *Podiceps nigricollis* that moult on the Great Salt Lake, Utah, USA encapsulate elements of wetland selection that likely characterise a moulting site for waterbirds during remigial moult, namely the flat trophic structure of a hyper-saline lake with little emergent or submersed vegetation means aquatic or aerial predators are rare or non-existent, and the protein content of the super-abundant and highly accessible prey (in this case the Brine Shrimp *Artemia franciscana*) in the lake provides optimal conditions for obtaining energy and nutrients for feather growth (Jehl 1990; Wunder *et al.* 2012). Flightless waterbirds constrained to a wetland minimise depredation by diving in the case of ducks or, as in the case of dabbling ducks, geese and swans, escaping terrestrial mammals by swimming into vegetation or open water distant from shore. Prior to remigial moult, birds must select habitats that fulfil their nutritional needs, specifically those for energy and protein with specific amino acids (Murphy & King 1984a,b). Given the need to meet normal energy and protein requirements, plus the extra needs of wing moult, and avoidance of predation whilst unable to fly, how do moulting waterfowl select their moulting habitats? Specifically, with regard to improving conservation and management options to protect and enhance such habitats, what are the key features of these habitats? Answering these questions is difficult, because few studies have ever specifically examined habitat use and selection by moulting waterfowl, in the sense that a particular feature or features are selected over others. Early examples attempted to describe the physical, floristic, and invertebrate features within sites that attracted, for example, moulting Green-winged Teal *Anas crecca* (Kortegaard 1974), but rarely have researchers investigated habitat use before, during and following the remigial moult to enlighten factors affecting habitat choice at that critical period. Thus, while we can describe habitats used by moulting waterfowl, there is insufficient literature available to relate use to available habitats to infer preferences or selection (*sensu* Kaminski & Weller 1992; Kaminski & Elmberg 2014).

In this review, we adopt a comparative approach among waterfowl taxa to examine habitat selection in relation to strategies that fulfil the needs for energy and protein during the remigial moult, while minimising risks to survival posed by flightlessness. Those few studies that exist suggest that safety from predators is paramount in the selection of habitats for moult but food resources and availability are also likely to be critical. Nonetheless, numerous questions remain. What general features can we distinguish about moulting sites that are similar or different from habitats used at other times of the annual cycle? How can identification of these features help us understand the potential process of habitat selection by moulting waterfowl? Can existing variation within and among species be used to address survival and possible fitness consequences of selecting specific habitats? Lastly, how do answers to these questions provide insight into how the conservation and management of moulting habitats might be improved for indigenous waterfowl in the northern hemisphere? Intuitively, moult is not independent of other annual cycle events and is highly dependent on reproductive investment and outcome (*i.e.* whether an individual is paired or unpaired, a breeder or non-breeder, a successful or unsuccessful breeder). Thus, we also attempt to assess how this may influence habitat use during remigial moult and the manner in which moult is completed. Finally, we consider the future key policy, conservation, and research needs in this arena. We start by considering the evidence for selection of habitats based on safety from predation and assess the specific energetic and nutritional needs of remigial moult. The focus is on remigial moult rather than body plumage moult, because both occur simultaneously during the summer moult into the eclipse plumage in the northern hemisphere (Weller 1980) and the period of flightlessness while remiges are lost and regrown and associated habitat and resource use by waterfowl are most crucial to individual survival and future fitness prospects.

Role of predation during remigial moult

The limited evidence available suggests that survival during the post-breeding and remigial moult is the same, if not greater, than during other periods in the annual cycle for such species as Mallard *Anas platyrhynchos* (Kirby & Cowardin 1986), Mottled Duck *A. fulvigula* (Bielefeld & Cox 2006), Black Duck *A. rubripes* (Bowman 1987), Wood Duck *Aix sponsa* (Thompson & Baldassarre 1988; Davis *et al.* 2001), Harlequin Duck *Histrionicus histrionicus* (Iverson & Esler 2007), Barrow's Goldeneye *Bucephala islandica* (Hogan *et al.* 2013a) and scoters *Melanitta* sp. (Anderson *et al.* 2012). However, survival probability by itself does not imply that predation risk has no role in shaping habitat use by post-breeding moulting waterfowl as it may simply indicate that waterfowl have mitigated this risk through adaptations.

Indeed, there are reports of flightless Pink-footed Geese *Anser brachyrhynchus* being depredated by Walrus *Odobenus rosmarus rosmarus* in Svalbard (Fox *et al.* 2010) and flightless moulting Common Eider *Somateria mollissima* and Greylag Geese *Anser anser* being pursued by Killer Whales *Orcinus orca* in the Shetland Islands, Scotland (D. Gifford, *in litt.*). Interestingly, both situations relate to expanding Palearctic populations of geese moulting in newly colonised areas, where local terrestrial moulting habitats have become saturated as a result of increasing local density. These examples may therefore be atypical in the sense that these populations have yet to reach fitness equilibrium with regard to colonisation of formerly unoccupied territory and exposure to novel predators. In the case of Mottled Duck, drying wetland conditions in peninsular Florida in late summer concentrate wildlife, including alligators *Alligator mississippiensis*, in and around remaining wetlands, resulting in alligator depredation of post-breeding moulting Mottled Duck (Bielefeld & Cox 2006).

An exception to "normal" survival rates during moult is the periodic occurrence of mass mortality due to diseases frequently occurring during moult and summer drought periods (Bellrose 1980). Dabbling ducks exposed to botulism during the post-breeding period may suffer severe mortality (*e.g.* > 350,000 Northern Pintail *Anas acuta* in prairie Canada, Miller & Duncan 1999 and < 12,000 Mallard, Fleskes *et al.* 2010; Evelsizer *et al.* 2010), as have Redhead *Aythya americana* (> 3,000 at one site, Wobeser & Leighton 1988) and sea ducks have suffered mortality related to virus exposure (Hollmén *et al.* 2003), although other die-off events may have been the result of contaminant exposures (Henny *et al.* 1995). The flocking behaviour of moulting waterfowl may facilitate disease spread within groups, and large mass mortalities are likely to have population level effects (Reed & Rocke 1992), but these events are rare and are unlikely to represent a major factor in moult ecology and site selection.

Factors that mitigate or reduce mortality during moult

Moult migration

Ecologists have hypothesised that an advantage of moult migration is selection of habitats with lower predation pressure or less diverse predator communities (Salomonsen 1968). In many species of ducks and geese, moult migrations are to higher latitude locations where predator populations may be numerically, or more seasonally, constrained (Yarris *et al.* 1994). For sea duck species, moult migrations may or may not represent an increase in latitude, but almost always represent a movement to marine areas where predators are fewer. Thus, moult migration itself may represent an adaptation to minimise mortality during the flightless period.

Flocking behaviour

Factors affecting abundance of moulting birds at a given site have not been explored. Most, if not all, waterfowl species moult in flocks that vary in size from a few birds to thousands of individuals. Solitary moulting does not seem to have evolved in any waterfowl species, although northern breeding female ducks completing brood rearing late will moult alone. In general, birds in groups are less susceptible to predation than solitary birds and safety is, to some degree, proportional to group size and to position within the group (Petit & Bilstein 1987; Elgar 1989; Tamisier & Dehorter 1999; *cf.* Davis *et al.* 2007). Leafloor *et al.* (1996) reported social interactions tend to synchronise moult timing in captive female Mallard and that this may have important survival advantages. The group response of moulting waterfowl to disturbance events suggests that one of the advantages to moulting in flocks is the increased detection of potential predators (Kahlert 2003). Thus, flocking behaviour may have survival advantages in spite of the potential for increased competition for food and more rapid pathogen transmission.

Behavioural activity also affects group size. Foraging flocks of moulting waterfowl are usually much smaller than roosting flocks which can aggregate thousands of individuals (Reed 1971; Jepsen 1973; Joensen 1973). Roosting in dense flocks likely has important bioenergetic and predator protection advantages. Moulting Surf Scoter *Melanitta perspicillata* (O'Connor 2008) and King Eider *Somateria spectabilis* (Frimer 1994) stop feeding when disturbed and regroup in large flocks offshore, a behaviour common to most moulting sea ducks and divers and some dabbling ducks (Oring 1964). Similarly, resting flocks of flightless Red-breasted Merganser *Mergus serrator* are larger than foraging flocks (JPLS unpublished data). The tendency of flocked birds (diving and sea ducks) to dive synchronously to feed may be an anti-predator or a foraging efficiency strategy (Schenkeveld & Ydenberg 1985). Certainly, simultaneous diving is a typical response to avian predators (PLF pers. obs.). Some species, especially dabbling ducks, rely on cover for protection and disperse in vegetation when disturbed. In some species of sea ducks, females often moult in smaller groups than males and may use different habitats (Gauthier & Bédard 1976; Jepsen 1973; Diéval 2006; Diéval *et al.* 2011). Dabbling ducks seem to rely more on cover during the remigial moult, and unlike some sea ducks, tend to form smaller flocks during remigial moult than before or after this period (Kortegaard 1974).

Selection for escape habitat

Moulting birds may show stronger selection for escape mechanisms as opposed to foraging habitat. For example, most northern geese moult in treeless areas and moulting concentrations can reach thousands of birds, where terrestrially feeding birds rely on adjacent open-water rivers, lakes, and other wetlands for escape from predators (Derksen *et al.* 1982; Madsen & Mortensen 1987). For these arctic geese, the primary predator influencing forage behaviour was likely Arctic Fox *Alopex lagopus*. Fox & Kahlert (2000) and Kahlert (2003) found that moulting Greylag Geese only foraged in close proximity to water (*i.e.* escape habitat) even though abundant unexploited forage of equal quality was available in other locations. Thus, these geese seem to be selecting for open habitats with good visibility but restrict their habitat use based on access to escape habitat from the local predators, although predators actually were absent during the study (Kahlert *et al.* 1996). In contrast, moulting ducks spend most of their feeding and roosting times on water where predators may harass and attack them from the air or under water. Dabbling ducks rely on emergent vegetation for concealment and escape and select lakes and marshes with presence of emergent vegetation (Kortegaard 1974; Fleskes *et al.* 2010). Moulting diving ducks escape danger by diving and dispersing and select wetlands of sufficient depth to avoid aerial predation. Thus, most dabbling ducks select habitats with emergent vegetation to moult whereas moulting diving and sea ducks generally avoid them and favour open areas (Oring 1964). However, predation on flightless Common Eider by Killer Whales has been documented (Smith 2006; Booth & Ellis 2006) indicating bird vulnerability to marine predators. Most sea ducks moulting in coastal waters forage at shallower water depths when flightless, perhaps linked to their impaired diving capacities as most use their wings underwater (Comeau 1923). Selection of shallow water may reduce the amount of time spent foraging and possibly minimise heat loss during submergence in cold waters. Further, use of shallow waters may be a strategy to minimise predation as water depth may limit exposure to some marine mammals (*e.g.* Killer Whales). In the extreme, some moulting Kerguelen Pintail *Anas eatoni* apparently moult in a cave on the Kerguelen archipelago to escape predation (Buffard 1995).

Behavioural modifications

Numerous studies have also documented general behavioural shifts associated with moult that might influence predation risk (Hohman *et al.* 1992). In general, moulting waterfowl reduce active behaviours and spend more time roosting (*e.g.* Döpfner *et al.* 2009; Portugal *et al.* 2011). The degree to which this behavioural modification is adopted is likely linked to energy balance, body mass dynamics and ability of birds to store reserves prior to moult. Nonetheless, by minimising time in potentially less safe habitats (*i.e.* foraging habitats) and selecting relatively safe roosting habitats, moulting birds may be minimising predation risk.

Minimisation of flightless period

Several studies have suggested that body mass dynamics of moulting waterfowl represent an adaptive mechanism to minimise length of the flightless period (Douthwaite 1976; Brown & Saunders 1998; Owen & Ogilvie 1979). The logic is that wing loading ultimately determines ability to fly. Therefore, mass loss during moult reduces wing loading and allows birds to regain flight before primaries are fully grown. For many species, mass loss may allow birds to gain flight when primaries are about 70% of ultimate length (Taylor 1995; Howell 2002; Flint *et al.* 2003; Dickson 2011). If flightlessness itself increases mortality risk, then this adaptation to minimise the flightless period would be an adaptation to reduce mortality. Interestingly, there are some species (*e.g.* scoters) which have protracted flightless periods and corresponding high survival (Anderson *et al.* 2012). These species have slow rates of feather growth and no mass loss while flightless (Dickson *et al.* 2012). As such, there appears to be little selective pressure to minimise the flightless period for scoters because they use habitats with adequate food and encounter little apparent risk of predation, although we cannot ignore the alternative hypothesis that these ducks need full wing length to fly.

Role of food

Is there a high energetic cost of remigial moult?

Replacing feathers is energetically costly, so waterfowl face potentially increased energy demands to meet the costs of feather growth (Payne 1972; Thompson & Boag 1976; Dolnik & Gavrilov 1979; Qian & Xu 1986; Portugal *et al.* 2007), estimated at 1.3 times basal metabolic rate in Mallard (Prince 1979). However, most species moult at the warmest point in the annual cycle and other factors suggest that the costs of feather replacement are not necessarily difficult to meet from external sources. For example, many waterfowl engage in the moult of body feathers synchronously with remiges (Weller 1980; Taylor 1995; Howell *et al.* 2003). Further, many species restrict food intake during moult compared to other times of the year. Finally, while many species lose mass during moult which could indicate an inability to balance energy intake with demand, this is not the case for all species or sites (Lewis *et al.* 2011a,b; Dickson 2011). Accordingly, moult is potentially a time period of energetic constraint, yet it appears that waterfowl have adapted to mitigate this cost.

Mass loss, what does it mean?

There has been debate as to whether mass loss during remigial moult in waterfowl is:

(1) an adaptive trait, whereby fat stores provide an endogenous source of energy to regrow feathers as rapidly as possible whilst reducing reliance on external energy sources, access to which

potentially increases predation risk (as suggested for some geese; Fox & Kahlert 2005);

(2) a simple reflection of the elevated energetic costs of feather synthesis which birds meet by catabolism of body "reserves" (the energetic stress hypothesis; Hohman 1993) rather than body "stores" acquired exogenously prior to the moult (*sensu* van der Meer & Piersma 1994);

(3) due to predation risk, that imposes cryptic feeding behaviour and exploitation of habitats where foraging is less effective, such foraging constraints necessitate exploitation of fat (which does not necessarily preclude pre-moult accumulation of fat stores; Panek & Majewski 1990); or

(4) an adaptive trait to reduce the length of the flightless period because lighter body mass enables Anatidae to regain flight earlier on incompletely re-grown flight feathers earlier than if heavier (Douthwaite 1976; Owen & Ogilvie 1979; Brown & Saunders 1998).

For at least one population of Mallard, Fox *et al.* (2013) showed (using supplementary feeding) that there was no support for (2) and (3) above and that (4) alone was not the primary factor that shaped weight loss. Rather they considered that the accumulation and subsequent depletion of fat stores, together with reductions in energy expenditure, enables Mallard to re-grow feathers as rapidly as possible by exploiting habitats that offer safety from predators, but do not necessarily enable them to balance energy budgets during the flightless period of remigial feather re-growth. In other words, both sexes of Mallard showed prior mass gain (mostly fat stores) to fuel energy demands during wing moult, just as migratory populations accumulate such stores to fuel migration. Male and non-breeding female Mallard could meet up to 82% of all energy expenditure whilst flightless from energy stores alone, and Pochard *Aythya ferina* could derive up to 92% of such energy demands (Fox & King 2011). Fondell *et al.* (2013) also provided evidence against (2) as Black Brant *Branta bernicla nigricans* with access to the most nutritious forage lost the most mass. However, Lewis *et al.* (2011b) emphasised that the adaptive relationship described in (1) is not fixed, as the overall rates of mass loss declined across several decades for moulting Black Brant.

Many species show mass loss during flightlessness (see review in Hohman *et al.* 1992 and references therein), including temperate moulting Greylag Geese. On the Danish island of Saltholm, their mass loss equated to depletion of fat stores accumulated prior to moult and which again could support a large proportion of the energy expenditures during moult if the geese opted not to move between safe resting areas during daylight and their night-time feeding grounds (Kahlert 2006a). Through hyperphagia, male Northern Shoveler *Anas clypeata* accumulated reserves prior to moulting and used stored resources to grow feathers, an adaptation to declining cladoceran availability in mid-summer (DuBowy 1985). However, even within a species, not all populations lose mass at the same rate implying that, while overall mass loss may be adaptive, there is some influence of local feeding conditions (Fox *et al.* 1998; Fox & Kahlert 2005; Fondell *et al.* 2013).

Factors that mitigate or influence energetic costs and mass loss

Meeting protein needs during remigial moult

Flight feathers comprise *c.*0.7% of the total body mass of a Greylag Goose (A.D. Fox, unpubl. data) and 0.2% of a female Mallard (Heitermeyer 1988) and remiges some 25% of feather mass, so while a substantial part of overall plumage, the absolute mass of flight feathers is relatively not that great. However, the simultaneous replacement of the largest feathers of most waterfowl over a relatively short period necessitates access to food that provides the basic nutrients for their synthesis. This includes amino acids containing sulphur for β-keratin synthesis (Hohman *et al.* 1992), which are generally less common in avian tissues and diet than in feathers (Murphy & King 1982, 1984a,b). The extent to which protein invested in feather tissue is derived from exogenous versus endogenous sources in moulting waterfowl remains unclear, but the only study (Fox *et al.* 2009) suggests both sources are used. Recent studies suggest a progressive change in isotopic composition, shifting from largely endogenous sourced protein to protein derived from the diet along the length of the feather as moult migrant geese come into equilibrium with a new isoscape (S. Rohwer pers. comm.).

Studies of the diet of moulting Greylag Geese on Saltholm showed there was selection for the most highly digestible and protein-rich species available; as the quality of this forage declined, the diet became increasingly diverse (Fox *et al.* 1998). However, that same study showed that birds exploited the best quality forage that was closest to open water to which birds could escape when threatened; leaving food resources distant from the water's edge unexploited, strongly suggested that predation risk during flightlessness was more important than simply food supply (Fox & Kahlert 2000, even in this case, where predators are absent, geese still responded vehemently to predator-like stimuli, Kahlert 2003, 2006b). However, in the case of moulting Greylag Geese on Saltholm, stable isotope data evidenced that geese used protein accumulated on the mainland in Sweden for feather synthesis (Fox *et al.* 2009). Proteins were released from organs which change in size during moult (Fox & Kahlert 2005), and excretion of nitrogen in the form of urea and uric acid nearly ceased during the middle part of moult suggesting considerable physiological mechanisms that reduced reliance on external sources of nitrogen during wing moult (Fox & Kahlert 1999).

Meeting lipid needs during moult

Lipids accumulated prior to moult are primarily used to meet elevated energy demands during moult to offset the temporarily increased demands of feather synthesis (Young & Boag 1982; Fox & Kahlert 2005; Fox *et al.* 2008). Many dabbling ducks (*e.g.* DuBowy 1985; Sjöberg 1988; Panek & Majewski 1990; Moorman *et al.* 1993; King & Fox 2012) and diving ducks (*e.g.* Fox & King 2011) lose mass during the flightless moult (*cf.* Fox *et al.* 2008; Dickson 2011; Hogan 2012; Hogan *et al.* 2013b), likely due to consumption of body fat stores. As in the case of Saltholm moulting Greylag Geese (Fox & Kahlert 2005), Folk *et al.* (1966) reported mass loss in moulting Mallard, and Young & Boag (1982) documented a reduction in fat stores in Mallard through moult, although they asserted there was no overall change in total carcass lipids, total proteins, or total body mass. However, Panek & Majewski (1990) showed 12% declines in body mass amongst males and females through moult. Taylor (1993) reported that moulting Black Brant lost 71–88% of stored lipid reserves and ended moult with only structural lipids remaining (*i.e.* 2–4% of fresh body mass).

So why do some Anatids lose mass during moult, while others do not? Not only can using fat stores potentially free moulting waterfowl from feeding or at least as intensively as would otherwise be necessary (*e.g.* Fox & King 2011) but there is also evidence from the difference in energy stores between moulting individuals that energy stores may affect the rate of feather growth. In Barrow's Goldeneye, van der Wetering & Cooke (2000) found that remigial growth rate in recaptured individuals was positively correlated with size-adjusted body mass at initial capture and that the daily rate of body mass loss was greater amongst birds that started moult in better condition. Hence, the lipid status in which an individual starts moult may have considerable implications for rate of feather growth (and hence duration of flightlessness) and may also be a function of the environment in which it moults to meet needs of maintenance and feather replacement.

Other species, such as some arctic moulting geese, unconstrained by feeding restrictions because of diel light conditions during summer (Fox *et al.* 1999), or sea ducks, such as the Common Scoter *Melanitta nigra* that live on protein and energy-rich food and occupy habitat that subsequently is the source of its winter food supply (Fox *et al.* 2008), show no such accumulation of fat stores in advance of wing moult and appear entirely able to supply their energy expenditure from exogenous sources during moult. Indeed, Canvasback *Aythya valisineria* males can actually accumulate mass in the form of lipid stores from exogenous sources toward the end of remige growth in preparation for autumn moult into breeding plumage, presumably because they undertake remigial moult in habitats with high food quality (Thompson & Drobney 1996). Surf and White-winged Scoter *Melanitta deglandi* moulting in coastal British Columbia and Alaska also gained weight during their remigial moult. Barrow's Goldeneye moulting on arctic wetlands lost weight during remigial moult (van de Wetering & Cooke 2000) but those moulting in northern Alberta gained weight (Hogan 2013b) suggesting high variability in moult ecology within species, perhaps linked to the time constraints imposed on birds in these different biogeographic settings.

Furthermore, the evidence presented above suggest Mallard under certain circumstances do not lose mass during moult (*e.g.* Young & Boag 1982), and there is evidence that Greylag Geese in the north of their range in Iceland and northern Norway lose far less mass than do those on Saltholm (Arnor Sigfusson, Carl Mitchell and Arne Follestad, pers. comm.). Rates of mass loss in Black Brant have varied through time such that birds moulting on the same lakes now lose less mass compared to several decades ago, suggesting that this trait is highly adaptive and may depend on local circumstances associated with the specific moult site and individual status (Lewis *et al.* 2011b). Hence, moult mass dynamics appear to vary within species with site and potentially reproductive status.

Data from moulting Black Brant from three different areas (*i.e.* brood-rearing flocks, failed breeding birds on the Yukon Delta, and failed- or non-breeding birds from Teshekpuk Lake) show major differences in mass dynamics before and during moult (Fondell *et al.* 2013, see Table 1 for an overall summary). Subjectively, forage varied across these three groups, with little forage available near the nesting colony for brood rearing birds, intermediate levels of forage available to failed breeding birds on the Yukon Delta, and abundant food available near Teshekpuk Lake for the moult migrant functional non-breeders. However, adults rearing young did not lose mass during moult. Failed breeding birds on the Yukon Delta lost intermediate amounts of weight during moult and those at Teshekpuk Lake lost the most. In these cases, mass loss was negatively correlated with apparent forage availability, yet mass at the onset of moult also varied across these three areas and was linked with the forage available at each area. So successful breeding birds started moult at a relatively low mass and

Table 1. Summary of moult behaviour of discrete elements of the brant population from the Yukon-Kuskokwim Delta in Alaska, showing the location, duration of flightlessness, mass dynamics and food quality of the habitats used for brood-rearing parents, failed- and non-breeding birds (Singer *et al.* 2012; Fondell *et al.* 2013).

Population segment	Moult site location (days)	Flightless period (mm/day)	Feather growth rate	Starting body mass	Food quality	Mass loss during moult
Brood rearing parents	At colony (few km)	30	5	Low	Low	None
Failed breeders	Yukon Delta (many km)	21	7.5	Inter-mediate	Inter-mediate	Little
Non-breeders	Teshekpuk (950 km)	21	7.5	High	High	Most

maintained body mass, whereas moult migrants started at a higher mass and lost most of that during moult. Thus, all groups converged on a similar mass at the end of moult. This convergence would suggest that mass loss is adaptive in that there is some optimal mass that reduces wing loading and facilitates flight and dispersal. These data suggest that there would appear to be some selection pressure to minimise the length of the flightless period. It is also interesting that moult migrants start at the highest mass implying that they are more than able to make up for the energetic costs of migration and perhaps bring fat stores as a hedge against uncertain food resources at the ultimate moult destination.

Black Brant rearing broods delay the onset of moult until about 16 days after hatch, thus regaining flight at about the same time as goslings fledge (Singer *et al.* 2012). So for waterfowl that stay with their broods, there may be little selective pressure to reduce the length of the flightless period because there is little advantage to adults flying before their young. Failed- and non-breeding birds utilise available forage to gain mass prior to moult. They can use supplementary body fat stores potentially to invest in more rapid growth of flight feathers (compared to the brood-rearing adults) to allow an early return to flight. However, female ducks raising broods face a trade-off between protecting the brood and departing with sufficient time to complete remigial moult in appropriate habitats.

Forage resources

In previous sections on the energetic dynamics of moult, we described a range of species that showed fat store accumulation prior to moult, where these stores were depleted as feather regrowth proceeded. This strategy may be an adaptation toward energetic independence from exogenous energy-rich foods in situations where foraging brings accompanying predation risks. However, evidence indicated that the rate of depletion of fat stores varied with remigial growth rate and initial mass in some species, suggesting endogenous food stores could accelerate feather growth and reduce duration of flightlessness and predation risk. Hence, the presence of lipid body stores does not necessarily imply that moulting birds have reduced need for exogenous energy, because there are many examples of moulting birds selecting food-rich environments. For instance, at the Ismaninger Teichgebiet, a complex of fish ponds in Bavaria, Germany, where 3 out of 30 impoundments were left fishless, these ponds each attracted, on average, about 2,000 birds, mostly moulting Eared Grebes, Gadwall *Anas strepera*, Mallard, Pochard, Tufted Duck *Aythya fuligula,* Red-crested Pochard *Netta rufina* and Coot *Fulica atra*, compared to <100 moulting waterbirds on the remaining lakes stocked with Carp *Cyprinus carpio* (Köhler & Köhler 1998). The implication of this extraordinary difference in moulting waterbird density was that the abundance of macroinvertebrates and algae in the ponds without carp provided improved feeding conditions over those ponds with carp. Intriguingly, Northern Shoveler was the only species to show similar (but low) moulting densities on stocked and fishless lakes, likely because it is a pelagic dabbling duck specialising on filter feeding of macro- and micro-invertebrates (Ankney & Afton 1988). Amongst Gadwall at this site, both sexes lost relatively little body mass, which they recovered before the end of wing moult (Gehrold & Köhler 2013). This contrasts with the consistent loss of mass amongst both sexes of the same species at a moulting site in southeast England (King & Fox 2012). The unplanned Ismaninger Teichgebiet "experiment" strongly suggested that locally high densities of moulting waterfowl may react to a combination of factors in moulting habitats, but the high density of food in the fishless ponds may have overridden any anti-predator function.

The density of moulting Barrow's Goldeneye on 21 ponds of the Old Crow Flats, Canada, was positively correlated with total phosphorous levels (van de Wetering 1997) suggesting a positive relationship between goldeneye abundance and primary productivity of the wetlands. In northwest North America, large moulting concentrations of waterfowl are associated with highly productive large shallow boreal and sub-boreal lakes (Munro 1941; van de Wetering 1997; Hogan *et al.* 2011), large shallow boreal (Bailey 1983a,b) and arctic wetlands (King 1963, 1973) and coastal estuaries (Flint *et al.* 2008), while in Iceland, numbers of moulting Barrow's Goldeneye and Red-breasted Merganser were correlated positively with food abundance (Einarsson & Gardarsson 2004). Loss of the ability to fly not only affects the ability of birds to avoid predation, it also spatially limits the ability to gather food during the flightless period, which likely restricts the ability to exploit the best foraging conditions. Even where this is not the case, the physical constraint on movements likely enhances local depletion of food resources.

Feeding ecology may also impose constraints on the size of moulting flocks. In general, species feeding on shellfish moult in larger flocks than species feeding on mobile invertebrates, fish or vegetation. For shellfish feeding species, foraging in groups is not limited to the moulting season but occurs during non-breeding seasons when birds are gregarious. Common Eider moult in mussel rich habitats, such as in the Danish Wadden Sea and Kattegat where aggregations reach tens of thousands, while scoters moult in areas with large sandy subtidal areas rich in bivalve shellfish resources (Joensen 1973; Laursen *et al.* 1997). These numbers likely represent abundance at moulting locations as foraging flocks at moulting sites tend to be smaller than those later in the winter (Follestad *et al.* 1988; Rail & Savard 2003). Mergansers feed on fish and moulting flocks are usually smaller than those of scoters and eiders: Red-breasted Merganser flocks moulting in the coastal waters of Anticosti Island in the St Lawrence, Canada averaged 39 birds/flock with a range of 1–322 birds (Craik *et al.* 2009, 2011); Common Merganser *M. merganser* flocks moulting on fresh and salt water appear to be in a similar range of size (Kumari 1979; Pearce *et al.* 2009). Goldeneyes forage on invertebrates and also moult in smaller groups than scoters or eiders (Jepsen 1973; van de Wetering 1997). Freshwater diving and dabbling ducks that consume aquatic vascular plant material may rely on large beds of such plants to support them through remigial moult, where larger feeding resources attract dense flocks of moulting birds (Bailey 1983a,b).

Flock behaviour for moulting may actually enhance forage quality and quantity via positive feedback. This hypothesis is particularly true for goose grazing systems where regular foraging tends to maintain plant productivity at a higher biomass and prolong the peak of nitrogen content (Cargill & Jefferies 1984). Fox & Kahlert (2000, 2003) demonstrated that moulting Greylag Geese maintained both protein and biomass production at the greatest possible levels by frequent re-grazing of the sward. There are no similar documented positive feedback relationships for other forage systems (*e.g.* invertebrates) that would be relevant for other waterfowl; however, behavioural modifications like simultaneous diving may enhance feeding efficiency. Thus, for some species of waterfowl, flocking behaviour during the flightless period may actually increase forage quantity, quality, foraging efficiency, or a combination of these. Moulting waterfowl therefore seem to concentrate in areas of high forage abundance, hardly surprising as large aggregations of birds would require a concentrated food source, from which they may gain an additional advantage from the decrease in predation risk to individual birds.

Behavioural modifications

One means of rebalancing an energy budget burdened by the additional energy demands of major feather synthesis is to reduce other forms of energy and other nutrient expenditure. Birds replacing flight feathers conserve energy by not flying, which is the most expensive activity of all avian energy expenditure, usually estimated at 12–15 times basal metabolic rate in waterfowl (*e.g.* Prince 1979; Madsen 1985). In moulting Common Eider, Guillemette *et al.* (2007) showed that daily and resting metabolic rates increased by 9 and 12%, but also that flightlessness reduced daily and resting metabolic rate by 6 and 14%, respectively, helping to balance energy demands of feather synthesis. Indeed, many authors concur that moulting waterfowl are much more secretive, but also far more quiescent than in the period prior to and following flightlessness, reducing activity substantially (*e.g.* Adams *et al.* 2000; Döpfner *et al.* 2009) even in captive waterfowl fed *ad libitum* (Portugal *et al.* 2010), although these studies collected activity data only during daylight. Hogan *et al.* (2013a,b) reported that moulting Barrow's Goldeneye foraged primarily at night on one lake and diurnally on another, possibly in relation to prey behaviour and availability suggesting adaptability to local conditions but perhaps also due to greater vulnerability to predation on the smaller lake where they fed nocturnally, although they could not quantify this risk. Hence, by their lack of flight and generally reduced activities, moulting waterfowl can substantially reduce their energy expenditure during flightlessness.

In contrast to the general observations that flightless moulting waterfowl are less active whilst replacing feathers, an alternative strategy would be for birds to feed more or on more energy dense or nutritious foods to meet elevated needs of moult. This hypothesis has rarely been tested because of the paucity of studies in this field, but has certainly been advanced for Mallard by Hartman (1985) and seems to occur in moulting Steller's Eider which feed on more energetically rich prey during the remigial moult (Petersen 1981).

Strategies invoked during remigial moult may also differ between species (Döpfner *et al.* 2009): Mute Swans *Cygnus olor* reduced swimming activities but increased foraging during moult; Red-crested Pochard *Netta rufina* increased locomotion and feeding activities; and Gadwall and Tufted Duck spent less time foraging. However, nocturnal activities were not monitored during this study and it is known that Redhead and Red-crested Pochard feed primarily at night during remigial moult (Bailey 1981; van Impe 1985), which has been suggested to provide an exogenous source of energy to offset thermoregulatory costs during the coolest part of the 24 hour cycle. Future study of the diurnal and nocturnal activities and energy budgets of moulting waterfowl would be extremely valuable to enlightening our understanding of habitat use and selection by moulting waterfowl.

Physiological modifications

An alternative strategy would be for moulting waterfowl to reconstruct body parts to help meet the energetic needs of remigial moult, an aspect of phenotypic plasticity. In this way, organs or muscles that are costly to maintain are reduced in size to minimise energy consumption. Shorebirds are well-known for making radical and rapid adjustments to the digestive apparatus in response to food supply (Piersma *et al.* 1993) and during refuelling episodes on migration (Piersma *et al.* 1999a,b) and grebes adjust organ sizes to meet the energetic costs of migration (Jehl & Henry 2010, 2013) and muscle mass for those that moult (Piersma 1988). Maintenance costs consume the vast majority of normal energetic expenditures of an organism, and most internal organs (but particularly the liver and gastrointestinal tract) are energetically costly to maintain in a larger state than is functionally necessary (Ferrell 1988). Hence, the level of downsizing of organs that occurs in the Greylag Goose during moult on the Danish island of Saltholm is likely associated with energetic savings over and above the alternative explanation under the use-disuse hypothesis (Fox & Kahlert 2005). That study found reduction of 41% in intestine mass and 37% reductions in liver and heart mass during moult, although these were increasingly reconstructed as birds progressed toward completion of moult. In a study of high arctic Brant, Ankney (1984) found no such changes in liver or intestine mass through moult, but this phenomenon may be because arctic geese are more able to meet their energy demands from herbivory during moult than are Greylag Geese moulting farther south. Dramatic changes in digestive organ size have been described in other waterfowl undergoing remigial moult (*e.g.* DuBowy 1985; Thompson & Drobney 1996), but this aspect of energy conservation and the degree to which such plasticity in organs can contribute to reducing energy expenditure has been rarely studied.

There is also evidence of changes in

muscle size during moult. In Mallard (Young & Boag 1982), Long-tailed Duck *Clangula hyemalis* (Howell 2002), Black Brant (Taylor 1993), Northern Shoveler and Blue-winged Teal *Anas discors* (DuBowy 1985) flight muscle mass decreased and leg muscle mass increased consistently with the predictions arising from the hypothesis of phenotypic plasticity (see also Ankney 1979, 1984; Fox & Kahlert 2005). Despite major changes in muscle architecture, these tend not to contribute to major overall changes in body mass during flightless moult in most studied Anatidae (*e.g.* Ankney 1979, 1984; Thompson & Drobney 1996), so such changes are less easy to dissociate from the simple hypothesis of use/disuse.

Competition within and among species

Some moulting sites attract single species (*e.g.* Harlequin Duck or Steller's Eider; Boertmann & Mosbech 2002; P. Flint unpubl. data) whereas others are used by several species of waterfowl including dabbling, diving and even sea ducks. For example Ohtig Lake (5.5 x 2.5 km) in Alaska supports 20,000 moulting ducks of at least 10 species, as does Takslesluk Lake (19 x 6 km) which attracts 10,000 moulters (King 1963, 1973). When disturbed, birds form mixed species flocks and swim toward natural sanctuary habitats. These lakes obviously fulfil the diverse needs of these species, combining vast areas of shallow open water with dense shoreline cover. Even smaller lakes may attract several species. Moulting Barrow's Goldeneye often form loose groups with moulting Canvasback and scaup *Aythya* sp. when resting and tighter groups if disturbed (van de Wetering 1997). These associations seem based on selection of similar habitat by moulting species rather than attraction to sites used by a given species. However, species likely benefit from each other from protection in numbers. In northern Greenland, Common Eider and King Eider moult at similar locations but use different habitats with King Eider foraging in deeper waters (Frimer 1995). In northern Alaska, four species of geese utilise the large thaw lakes north of Teshekpuk Lake (Flint *et al.* 2008). However, there is some spatial segregation with different species using somewhat different areas. Even in cases where multiple species are moulting within the same watershed, we do not know if they compete for the same forage (Lewis *et al.* 2011b).

Selection of moulting habitats by sea ducks is likely based on food resources and on the presence of congeners. Thousands of eiders, scoters and Long-tailed Duck may use a given moulting site. Approximately 30,000 Long-tailed Duck moult along 531 km of coastline in the Beaufort Sea, dispersed among 73 areas supporting from a few to 2,500 birds, depending on local habitat configuration (*e.g.* presence of islands, sand spits; river deltas; Gollop & Richardson 1974). However, within that site they form several foraging flocks of various sizes. Flint *et al.* (2004) studied radio-tagged Long-tailed Duck moulting in lagoon systems and demonstrated that while flocks were consistently observed in the same locations, there was considerable turnover of individuals within some flocks. As such, aggregations could simply be the result of numerous individuals sampling and selecting habitat rather than benefitting from flocking behaviour. Hagy and Kaminski (2012) report for wintering dabbling ducks that they continue to sample and forage in emergent wetlands in spite of food depletion in the wetlands. Because waterfowl may not be able to assess food abundance without sampling, they continue to forage in patches to assess resource abundance. Forage sampling may be an adaptive strategy for waterfowl as a consequence of temporal and spatial dynamics of wetlands used by Anatids. Finally, almost nothing is known about social intra- and inter-specific interactions during moult, especially of interaction between males and females and between adults and sub-adults.

Habitat selection

Moult migration: selection of moult location at macro-scales

Given available food and safety from predation during the flightless moult period, the default setting for waterfowl ought to be to moult on summer areas, typically within the breeding range, to conserve energy expended in migrating. Yet despite this expectation, many waterfowl show a well-developed moult migration (Salomonsen 1968), and the review by Hohman *et al.* (1992) revealed a wide and bewildering range of moult migration strategies among and within species and populations. In North America, there is a general northward movement into boreal forest and tundra biomes and associated offshore areas, although notable exceptions to northward movements are resident species, female Anatids that successfully rear a brood, and some species such as scoter, King Eider, Northern Pintail, and some *Aythya* species that moult on or near the wintering grounds (Sheaffer *et al.* 2007; Luukkonen *et al.* 2008; Oppel *et al.* 2008). Ducks, geese and swans also aggregate in biologically productive areas in the arctic, such as major river deltas to regrow flight feathers, although such aggregations are also known from temperate regions (*e.g.* the Volga Delta for Northern Pintail; Dobrynina & Kharitonov 2006). Indeed, although great variability exists among Anatid moulting strategies throughout the northern hemisphere, habitat use and selection have evolved to promote individual survival and as rapid as possible growth of remiges to regain flight.

For many sexually immature, unpaired or otherwise non-breeding birds, the spring migration is functionally a moult migration, especially for males, because moulting is the only major annual-cycle physiological process experienced by these non-breeding individuals during spring and summer. In species with delayed maturation, sub-adult females often return to their natal grounds before moult (Eadie & Gauthier 1985; Pearce & Petersen 2009). North American Aythyini pair during spring, but all females probably return to their natal sites whereas males follow mates or use unfamiliar breeding areas hoping to invest in reproduction. Functionally non-breeding sub-adult geese may associate with parents before moving to other areas to moult. For the males of many dabbling and diving duck species, they are able to exploit the abundance of food in the northern spring and summer to undertake a moult migration away from the nesting areas early in the season after having acquired necessary body stores.

Reproductive success has a major influence on the timing of moult migration and moult, so while successful breeding geese moult with their offspring on natal grounds, male and female ducks rarely if ever do. Breeding failure is typically greatest during egg laying, early incubation, and early brood rearing in ducks, so the onset of the "post-breeding" period may be variable, depending on possible re-nesting effort and success and species-, sex-, and age-specific variation. Although individual waterbirds are flightless for 3–7 weeks (Dickson *et al.* 2012), not all individuals moult at the same time (Jepsen 1973; Austin & Fredrickson 1986; Hohman *et al.* 1992), so at some moulting locations flightless birds can be present over a period of 2–3 months (Dickson *et al.* 2012). Amongst ducks, sub-adults and unpaired adult males generally moult first, followed by paired males, unsuccessful breeding females and successful breeding females (Jepsen 1973; Joensen 1973; Savard *et al.* 2007; Hogan 2012). Breeding status also influences the timing and duration of moult as was shown in the example of moulting Black Brant in Alaska above (Table 1).

An early departure from nesting or brooding females, and an ability to acquire body stores and migrate to moulting habitats, enables male ducks to exploit productive habitats (not necessarily suitable for brood rearing) whilst avoiding intra-specific competition from brood rearing females and ducklings. Scoters breed on inland lakes but moult in coastal waters, frequenting habitats similar to those used during winter. Some populations even moult and winter in the same locations (Fox *et al.* 2008) but most do not (Bordage & Savard 1995; Savard *et al.* 1998). Even species that moult on or near breeding areas use different habitats. Moulting scaups and goldeneyes use larger lakes for moulting than during the breeding season. Colonial Common Eider that frequent coastal waters during their entire life cycle segregate brood rearing and moulting habitats (Dieval *et al.* 2011). Mergansers and Harlequin Duck that breed on rivers, typically avoid these habitats for moulting and regroup on larger lakes (Common Merganser) or in coastal waters (mergansers and Harlequins Duck; Pearce *et al.* 2009; Robertson & Goudie 1999; Mallory & Metz 1999). Adult female Common Merganser may moult with offspring in rivers in Alaska, but it is likely a rare event resulting from late nest initiation and success (J. Pearce, *in litt.*).

One of the earliest studies of waterfowl moult migration was by Sven Ekman (1922) who described movement of Lesser White-fronted Geese *Anser erythropus* uphill within the same area to moult. The same phenomenon was evident amongst Greenland White-fronted Geese *Anser albifrons flavirostris* in west Greenland, which exploited lowland wetlands during spring arrival and subsequent breeding period, but successively moved to plateau areas to moult (Fox & Stroud 1981). In both cases, this behaviour likely was a response to the successive delay in growth of plants at a higher altitude, because the Greenland

White-fronted Geese finally fed on the north facing slopes, the site of the most delayed plant growth around the lakes. In the west Greenland study area, adequate water bodies existed at all altitudes (*i.e.* offering safety from predation), but movement of foraging geese uphill suggested that food availability and quality were fundamental in choice of their moult habitat.

For most northern breeding geese, the period of moult occurs simultaneously with brood rearing period. Adequate moulting habitat exists in close proximity to the nesting grounds, yet non-breeding and failed breeding Greenland White-fronted Geese often moult in the same habitats but away from families (Fox & Stroud 1981). When such habitat is limiting within an area of the breeding grounds, food limitation may influence non- or failed-breeders to disperse to alternative moulting areas. Amongst Greenland White-fronted Geese, this circumstance involves the non-breeding or failed nesting birds moving uphill within their mountainous summer range to exploit the delayed thaw and plant growth at higher altitudes, thereby reducing direct competition from breeders and broods (Fox & Stroud 1981). A similar shift but on a far greater spatial scale is also evident amongst the Pink-footed Geese that breed in Iceland, where the non-breeding individuals undertake a moult migration to north eastern Greenland (Taylor 1953, Mitchell *et al.* 1999). In this case, travelling north to exploit the delayed arrival of spring growth, an area where the growing season is too short to support breeding birds. The same species shows an analogous shift in Svalbard, where the delay in thaw is along a west-east axis, with non- and failed breeders travelling to Edgeøya and moulting further east of the core nesting range (Glahder *et al.* 2007).

As migration often has some genetic basis (Berthold *et al.* 2003), the same likely is true for moult migration, albeit mediated by individual reproductive outcome and status. For example, translocated Canada Geese *Branta canadensis* established in Yorkshire, England undertook an apparently innate, northward moult migration to Scotland (Dennis 1964), perhaps as their conspecifics did on the North American continent. However, learning may be important as well, as demonstrated by the selection of new moulting locations. For example, the Yorkshire Canada Geese subsequently started to moult locally (Garnett 1980), as Canada Geese have started to moult in the salt marshes of the St. Lawrence Estuary in recent years (Canadian Wildlife Service unpublished data) and urban sites have been used by moulting Canada Geese for decades creating management problems (Breault & McKelvey 1991; Moser *et al.* 2004). Factors affecting the selection of a moulting location appear complex. Birds often fly thousands of kilometres to distant moulting areas, although they could moult in suitable nearby areas (Brodeur *et al.* 2002; Robert *et al.* 2008, Chubbs *et al.* 2008; Savard & Robert 2013). Some female Common Eider breeding in the Gulf of St. Lawrence moult along Anticosti Island, an important moulting location for about 30,000 eiders, located about 100 km from the colony but others from the same colony moult in Maine about 800 km away. Such discrepancies may reflect reproductive status of the females, or the time at which they abandoned their attempt to breed, not least because the timing of arrival to moult sites may affect the degree to which local density affects the decision to settle or not or could have some genetic basis. Nevertheless, how can these two vastly different strategies have equal fitness benefits, especially given the differential energetic investment needed to move between these different areas?

Most waterfowl exhibit site fidelity to their moulting location and even their moulting site within a location (Szymczak & Rexstad 1991; Bollinger & Derksen 1996; Bowman & Brown 1992; Breault & Savard 1999; Flint *et al.* 2000; Phillips & Powell 2006; Knoche *et al.* 2007), suggesting local knowledge about conditions during flightlessness may be an advantage and therefore also a factor in habitat selection. Equally, the reliability of appropriate conditions, such as food resources and lack of predation, is likely to favour return to specific areas (Salomonsen 1968). However, some individuals are known to change moult location between years. Female breeding philopatry, combined with winter pairing, means that drake waterfowl are likely to find themselves in very different locations annually at the end of egg laying (Peters *et al.* 2012). For example, a drake Northern Pintail might pair with a hen that nests in the prairies in one year and with one that nests in Alaska the next, confronting that individual with radically different moult migration conditions (*e.g.* geographical and nutritional) among years even when reproductive investment does not vary. This possibility is borne out by observation as well, for example, a moulting adult male White-winged Scoter, captured in the St. Lawrence Estuary, moulted on the Labrador coast the following year and in Hudson Bay during the third year, whereas five others returned to their previous moulting area in the St. Lawrence (JPLS, unpubl. data). Likely, age, sex, pairing status, reproductive success and body condition may all interact and affect selection of a moulting location (Jepsen 1973; Petersen 1981). In eastern North America, Barrow's Goldeneye moult in a variety of habitats from inland lakes to estuarine and even marine wetlands (Robert *et al.* 2002; Savard & Robert 2013). An adult female Barrow's Goldeneye moulted one year on an inland lake near James Bay, 930 km from her nesting area and the following year in the St. Lawrence Estuary, only 132 km from her breeding area (Savard & Robert 2013) indicating plasticity in choice of moulting location and habitat.

In many cases, moulting birds occupy habitats that are unsuitable for breeding birds because some critical component is missing (*e.g.* nesting habitat nearby) or season length is inadequate. However, in other cases, the habitat seems suitable, but breeding birds are geographically separated from moulting non-breeders. Generally family groups are behaviourally dominant over non-breeders and arctic nesting ganders, for instance, will aggressively displace non-breeding geese, despite being numerically outnumbered. But growing goslings require an abundance of high quality forage and broods cannot defend their entire home range from competitive foragers. Given that moulting locations are traditionally used and individuals show high site fidelity, non-breeding birds may have displaced breeders from these "optimal" habitats. This hypothesis avoids the "group selection" argument that is required to explain why moulting birds voluntarily abandon breeding habitats, if those breeding habitats are the best available.

Selection of the moult location at the intermediate scale

Given that birds have selected habitat at the large scale (*i.e.* via moult migration or not), they next select habitat at an intermediate scale in terms of actual moulting location. Functionally, this level of choice represents selection of the watershed or wetland complex and is likely to be the unit scale to which an individual shows high levels of inter-annual site fidelity. The scale of this selection is ultimately determined by wetland size, complexity, and continuity (Lewis *et al.* 2011a,b). Multiple studies have shown that individuals have generally high rates of fidelity to specific wetland complexes, implying generally consistent conditions across years; nevertheless, there are several examples where moulting birds have shifted distributions or colonised new areas over time (Flint *et al.* 2008).

Lewis *et al.* (2010a, b) examined pre-moult patterns of movements for Black Brant that had undergone a short distance moult migration. In that study, individual brant used a range of wetlands over a broad area before ultimately selecting a specific moult location. They concluded that patterns of movements were consistent with birds functionally prospecting for moult locations. In most cases, birds visited a range of potential moult locations, before returning to a previously used lake to moult. As such, site selection can have a fidelity component where birds show a preference for locations across years, but by prospecting multiple sites each year, they are able to detect potentially new high quality sites allowing them to adapt to habitat change (Flint *et al.* 2014).

Selection of moult location at the very fine scale

When birds have selected a wetland complex, how they utilise habitat within these areas during the flightless period represents their balance between nutrient acquisition for maintenance and moult and survival. Settlement at a local scale is more likely to reflect annual habitat and ambient conditions. For example hydrology, air and water temperatures, wind exposure, extent of escape cover, and food availability affect habitat selection at the fine scale, which as a result may show lesser levels of inter-annual site fidelity. Fox & Kahlert (2000) showed that food may be broadly distributed within moulting sites, but birds only utilised forage in close proximity to escape habitat. Lewis *et al.* (2011a) did not measure forage availability, but showed that moulting Black Brant used a home range that was a functional strip of foraging habitat along shorelines. Further, Lewis *et al.* (2011a) found a relationship between initial body mass and home range size such that birds with increased body mass had decreased home ranges. This pattern fits the notion that stored reserves are primarily used to minimise activity during the moult. Thus, moulting locations can range from a restricted locality of a few hectares to over hundreds of square kilometres, depending on body condition of moulting birds, the size and dispersion of suitable habitats (Joensen 1973; Gilliland *et al.* 2002), and the scale of resolution (*i.e.* Ungava Bay *vs.* Labrador coast; southern *vs.* eastern coast of Ungava Bay; "inlet A" *vs.* "inlet B"; *etc.*). Harlequin Duck moult along rocky coastlines and feed within a few metres of the tide line (Robertson & Goudie 1999). The configuration of their foraging habitat is basically linear imposing a limit on the sizes of home range and moulting flocks (usually < 50 birds). In contrast, moulting scoters and eiders forage mostly in subtidal zones at depths < 10 m, which vary greatly in area; thus, their home range size is likely determined by bathymetry and moulting flocks can reach thousands of birds.

Effects of disturbance

It has been noted that most species of waterfowl tend to moult in relatively undisturbed locations. While flocks were observed to respond strongly to disturbance stimuli, Lacroix *et al.* (2003) found no clear effect of a localised seismic survey on displacement of moulting Long-tailed Duck. In cases of persistent harassment, such disturbance may lead to drowning, considering flightless birds with incomplete plumage are less efficient divers, have lower thermal efficiency, and probably less buoyant than fully feathered birds. Comeau (1923) reported fishermen harassing flightless birds until they drowned. Derksen *et al.* (1982) reported that moulting geese formed tight flocks and immediately ran to water when disturbed. Further, Madsen (1984) and Derksen *et al.* (1982) noted that relatively low levels of human disturbance could cause moulting geese to abandon a wetland, but uncertainty exists as to what extent such disturbance and displacement might have on rates of site fidelity among years and individual survival. However, intentional regular disturbance precluded birds from moulting on specific wetlands in an urban environment (Castelli & Sleggs 2000). Thus, disturbance may play a role in habitat selection by moulting waterfowl with demonstrated displacement within years and potential for displacement among years. The thresholds and stimuli involved should be the focus of research attention in the future to improve our ability to undertake impact assessments and provide management recommendations.

Adaptation to change

There is little evidence that moulting habitats may be limiting, but habitat loss could potentially result in limits on moulting habitat availability. We have mentioned the expanding populations of geese that have fully occupied the available freshwater lochs as potential moult sites and have commenced moulting in marine waters where they are exposed to novel predation by marine mammals (Glahder *et al.* 2007). This phenomenon suggests exposure to a new source of mortality as a result of intra-specific competition and density dependent processes on land. We know little evidence to support the idea that inter-specific competition could also impose limitations on moulting birds. The only evidence comes from two studies of interactions between goose species moulting in the same arctic areas. The first is the study of Madsen &

Mortensen (1987), which showed that allopatric Barnacle Geese and Pink-footed Geese in Greenland fed on the same graminoid plants, but more moss occurred in the diet under sympatry, especially amongst Barnacle Geese. Barnacle Geese spent more time feeding in sympatry than when feeding alone, while Pink-footed Geese showed no change. The other case is the study of the interactions between the endemic Greenland White-fronted Geese in west Greenland and recently colonised Canada Geese *Branta canadensis interior* to this region. In this case, both species fed on similar plants in allopatry, but where they moulted together, Canada Geese showed no diet shift, whilst White-fronted Geese fed on lower quality forage, such as moss, and tended to feed on the periphery of areas where they would feed in isolation even though little overt aggression was witnessed between the species (Kristiansen & Jarrett 2002). Although such a shift in diet is not evidence of competitive interactions, such a mechanism may have fitness consequences, given that feeding at the study site was restricted to 200 m of the edge of water where food may have become limited because geese were reluctant to forage away from water to which they would retreat when threatened by predators such as Arctic Fox. Other studies of the same species, in extensive wetlands where feeding limitations may not be so manifest, found little evidence for such shifts in diet and no evidence of changes in local abundance of White-fronted Geese in the face of increasing Canada Geese (Levermann & Raudrup undated; Boertmann & Egevang 2002).

Moulting waterfowl are also faced with broadscale ecological changes as dictated by global climate or more localised weather dynamics (*e.g.* Pacific Decadal Oscillation, North Atlantic Oscillation; Schummer *et al.* 2014). Such changes may allow for range expansion or invoke range contraction. For example, distributional shifts of moulting geese along the Arctic Coastal Plain may have been caused by climatic ecological changes (Flint *et al.* 2008; Lewis *et al.* 2011b; Tape *et al.* 2013). Further, recent surveys document a substantial range expansion for moulting Black Brant in this area (Flint *et al.* 2014). Ground observations document an increase in grazing lawns along the coast and experimental manipulations demonstrate that longer, warmer summers likely increase forage plant productivity. Thus, environmental changes appear to have influenced the distribution and abundance of forage plants, and moulting geese have expanded their range accordingly.

Habitat loss and degradation are likely to become an increasing challenge, for example, as a result of loss of boreal forest habitat, changes in precipitation, oil and gas exploration. Yet we know almost nothing about how waterfowl adapt when wetlands and food resources used for moult are no longer available.

Post-moult requirements

We have already discussed the influence of age, sex, body condition, breeding success, and environmental resources on habitat selection during the flightless period. Further, wing moult does not appear to be a period of particularly high mortality, nor does it necessarily expose birds to unusually high energetic constraints. Nonetheless, moulting physiological ecology may have cross-seasonal effects on subsequent annual-cycle events. Here we consider the potential effects of post-moult requirements on habitat selection and body mass dynamics during the moult. Following wing moult, the next critical period in the life cycle of waterfowl is completion of the body moult (Pyke 2005) and fall migration and associated staging. Fifty years ago, Harold Hanson (1962) speculated that "…there could be little doubt that stress of remigial moult is particularly heavy on females, following the energy demands of egg laying and care of young. It seems possible that the apparent differential stress of moult may be a primary reason for the preponderance of males in populations of adult waterfowl". Hanson's general point is likely highly relevant for many female ducks that invest heavily (especially somatic lipids) in a clutch, incubation and rearing offspring, followed by the energetic challenges of remigial moult and hyperphagia in preparation for autumn migration. This has recently been confirmed in Mallard, where radio tracking of brood rearing females showed "…reduced survival of females that raise broods presumably resulted from insufficient time to moult and prepare for fall migration" (Arnold & Howerter 2012). The key point here is likely the "time" element. For Black Brant, brood rearing and failed or non-breeding birds moult on about the same date (9 July) but brood rearing birds have slower feather growth resulting in a longer flightless period (Taylor 1995; Singer *et al.* 2012). Given that Taylor (1993) demonstrated that non-breeding moulting Black Brant functionally exhausted all available stored lipids, brood rearing birds may not finish moult in worse condition. Thus, brood rearing birds may finish moult in comparable conditions, but at a later date leaving less time to rebuild reserves for migration. Therefore, the primary cost of wing moult for breeding birds is likely related to time between completion of wing moult and onset of fall migration.

Given time constraints, some portion of habitat selection during moult may be dictated by habitat needs immediately following wing moult. Lewis *et al.* (2010a,b) showed that Black Brant departed inland moulting lakes and moved to nearby coastal estuaries upon resumption of flight. Importantly, this shift occurred before flight feathers were fully grown. Thus, apparent habitat suitability changes when birds regain flight. They then stage in these coastal estuaries for several weeks before initiating autumn migration. This phenomenon raises the possibility that habitat selection during the moult was influenced by proximity of suitable staging areas or individual ability to exploit moult habitats that facilitate foraging and body condition to enable flight to more distant post-moult staging areas without fitness costs. Several studies have also demonstrated that while birds lose mass during the moult they begin to gain mass as soon as they regain flight (Brown & Saunders 1998; Howell 2002). The behaviour of birds following wing feather moult seems variable with some moving out of the moulting area (Lewis *et al.* 2010a,b) and others remaining at the same location until autumn migration (Brodeur *et al.* 2002; Robert *et al.* 2002). Some waterfowl also complete body moult at or near their wing moult location taking advantages of productivity of these sites. We know very little of this period of the life cycle of waterfowl. We believe that cross-seasonal effects are important factors in determining habitat use by moulting waterfowl, but we suggest that it is the period immediately following moult that likely has the greatest effect.

Conclusions

Post-breeding waterfowl appear to select moult habitats on the basis of avoiding: (i) predation whilst unable to fly, and (ii) the nutritional stress associated with flight feather replacement (especially amongst brood rearing female ducks). Indeed, habitats will be selected to reduce risk of mortality to an absolute minimum; this outcome is borne out by studies that confirm high survival during moult. Despite the apparent wealth of references cited here, this part of the annual cycle remains poorly studied and even less well understood, particularly with respect to habitat selection. Waterfowl show a remarkable array of structural and metabolic changes associated with moult which must confirm this period as critical to completion of the life cycle, because waterfowl remiges and plumages must be replaced annually. Different waterfowl species adopt a wide range of potential mechanisms to acquire adequate nutrients and energy to survive flight feather moult, presumably as rapidly as possible, without compromise to the quality of the feather structures (although this is not known) that must support the bird throughout the coming year. Increasingly, observations suggest moulting Anatidae reduce their general level of activity, yet whilst many authors speculate on the fitness costs of various behaviours during moult, none have actually shown the magnitude of the relative costs and benefits of these different strategies to survival and fulfilling the life-cycle. If a moulting waterbird drastically reduces feeding activity, what is the cost (in terms of reduced energetic intake) versus the gain (in terms of reduced energy expenditure and elevated survival probability)? With the exception of Kahlert (2006a, which could not address survival probability) there have been few attempts to empirically demonstrate the effects of adopting such strategies.

We should also consider that perhaps a very important factor in choosing a moult site is not merely that the individual emerges from remigial moult with a new set of flight feathers but also attains improved body composition, organ status, and condition for onward movement to the next stage in the annual cycle. We also suggest that researchers reconsider the interpretation of mass loss during moult. Generally, we find support for the hypothesis that mass loss is an adaptation to minimise the length of the flightless period. However, this review also demonstrates that local conditions influence rates of mass loss. Mass loss is variable within and among species, among years, locations, ages, sexes and breeding success. In cases where forage is abundant, mass loss may be behaviourally driven, stimulating birds to forage and complete moult at an increased rate. Conversely, when forage is inadequate, mass loss may be compulsory, but the associated early return to flight allows birds to seek more favourable conditions. Accordingly, we suggest that mass loss is a mechanism used by moulting waterfowl or a consequence of moulting and environmental conditions to adapt to variable constraints. As such, mass loss cannot be used to infer habitat limitation. An especially exciting research prospect would be to use manipulative experiments to see how movement from selected habitats to unoccupied ones might affect mass loss during wing moult. Samples of flightless birds could be captured and moved to similar but unoccupied habitats to compare survival, body mass dynamics, and behaviour with those left to remain at selected habitats. Such approaches might also challenge the notion that social dynamics combined with site fidelity may have reduced the possibilities of colonization of potentially suitable moulting habitats not currently exploited.

Finally, our narrow focus on remigial moult in this review has perhaps had the effect of emphasising loss of flight (and the associated survival risks and foraging challenges) at the expense of nutritional aspects of body moult in the Anatidae generally. Completion of body moult (*i.e.* other than flight feathers) in other regions and other times of year also has important consequences for performance of other annual cycle events (not least for attracting a mate) and therefore fitness and deserves far greater research attention.

Conservation and management implications

What is clear from this synthesis is that there is no "one size fits all". We see different species with contrasting patterns in phenotypic plasticity and the ways they may go about reducing energy expenditure, whilst others (such as non-breeding arctic geese) have little difficulty in balancing energy budgets during the replacement of remigial feathers. Yet even within species, individuals may adopt different strategies at different stages of their own lives, dependent on breeding status, confirming that not all individuals or species have the same goals through to the end of moult. Faced with the challenges of moult, waterfowl may take multiple routes to achieve the same end. An individual selecting between these alternatives is likely to do so according to its internal state and the environmental factors that it encounters, so we need to better understand this part of the process before we can define concrete research/management options for specific species in specific situations.

Faced with such massive variation and uncertainty, but confronted by an urgent need to think about developing conservation policy to address the needs of waterfowl moult, we suggest some priorities for actions in the immediate future. The first is to define moult habitat for each population flyway and identify the larger or most sensitive concentrations (but beware the likelihood of rapid changes in feeding ecology and use of moulting resorts, *e.g.* Nilsson *et al.* 2001). Such a simple inventory exercise, to know "how many and where", would provide a framework for establishing site-safeguard networks and potentially identify critical habitat types to ensure these figure prominently in the design of site safeguard networks as well as in land-use planning and environmental impact assessment where these habitats are threatened. The second priority is to attempt to define the moult strategies for each population, for example determining if the various subsets of a species are moult migrants, depend upon fat stores for energy supply or on local resources. Particular focus should be placed upon breeding females, because of the nutritional and energetic stresses on them following incubation and brood rearing, and the specific implications of their moult patterns for habitat protection, protection from disturbance and hunting. This will affect whether site safeguard and/or protection from disturbance is more important to be implemented on the moulting grounds or on the post-breeding pre-moulting habitats where fat stores are accumulated. It is also important to: 1) assess the degree of wetland loss and global change (including climate) that affect moult behaviour and distribution, 2) determine the effects of internal state specificity on the strategies adopted by different individuals at different stages of the life cycle, 3) design site safeguard and habitat management programmes to optimise the availability and suitability of moult habitat along the flyways of the northern hemisphere but that can also accommodate change, and 4) define relationships between breeding, moult and wintering locations (pooling present and future knowledge from satellite telemetry studies for example).

Management implications and policy needs

Moulting waterfowl are sensitive to disturbance and therefore show enhanced susceptibility to human activities that increasingly encroach on moulting habitats. However, we still know very little about threshold levels that can effect change, such as shifts in moulting location or strategies between seasons as a result of disturbance. We know that this happens, because there are documented cases of Greylag Goose moulting grounds being completely abandoned from one year to another (*e.g.* Nilsson *et al.* 2001). These aspects need to be the subject of much greater study to establish management prescriptions for more effective management of moulting sites where human disturbance is a factor in affecting carrying capacity. There are some indications that flightless sea ducks are extremely vulnerable to disturbance, especially because of their reduced diving capacities (Comeau 1923), thus moulting sites may need special consideration. The exploitation of moulting flocks for subsistence occurred in the north (King 1973) but its current level is unknown as is its impact at the population level. Little work has been done on the carrying capacity of moulting locations and its annual variability, yet such knowledge is essential if we are to be able to provide management advice in generic or specific case of conflict. Gill net fisheries at important moult sites should be managed to avoid by-catch casualties. Also contingency plans are needed at all important moulting locations to minimise the impact of possible oil spills. Northern moulting locations both inland and coastal have not all been identified. As northern development is likely to increase as a result of climate warming it is urgent to identify all sites of particular significance to flyway populations. In particular, there are increasing pressures on boreal forest, near-shore, and arctic biomes posed by mining, oil and gas exploration and exploitation, agriculture, timber harvest, direct and indirect (*e.g.* transport, contaminants) impacts of oil, disease and contaminants, and the general increase in accessibility to these areas that brings associated levels of disturbance and recreational pressures.

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