Non-breeding habitat preference affects ecological speciation in migratory waders

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Abstract Models of ecological speciation predict that certain types of habitat should be more conducive to species diversification than others. In this study, I test this hypothesis in waders of the sub-order Charadrii using the number of morphological sub-species per species as an index of diversity. I classified all members of this clade as spending the non-breeding season either coastally or inland and argue that these represent fundamentally different environments. Coastal mudflats are characterised by high predictability and patchy worldwide distribution, whilst inland wetlands are widespread but unpredictable. The results show that migratory species that winter coastally are sub-divided into more sub-species than those that winter inland. This was not the case for non-migratory species. I argue that coastal environments select for more rigid migratory pathways, whilst inland wetlands favour more flexible movement patterns. Population sub-division could then result from the passive segregation of breeding sites or from the active selection for assortative mating of ecomorphs.

Keywords Speciation . Waders . Non-breeding habitat . Sub-species

Introduction

Models of ecological speciation show that the propensity of a species to diverge is affected by the shape of the fitness landscape generated by its environment (Gavrilets 2004). This predicts that some environments should be more conducive to speciation than others. Recent comparative studies have supported this prediction (Funk et al. 2006; Phillimore et al. 2007). However, these studies do not discuss aspects of habitats that promote or inhibit speciation.

In this study, I test this prediction for wading birds of the sub-order Charadrii. This group was chosen because its species can be divided into those that are adapted to coastal habitats and those that feed mostly inland (Piersma 1997, 2003). On a year-to-year basis, coastal habitats offer a more predictable environment than inland wetlands (Roshier et al. 2001). Inter-tidal mudflats and ocean beaches will be located in the same place each year and offer a highly predictable pool of food resources. They are distributed patchily around the globe, and patches differ in their food resources and other conditions (Piersma et al.1993a). On the other hand, the inland wetlands favoured by other waders are unpredictable and include waterbodies in arid regions that flood infrequently. Flooded areas are often large, but may be located in different areas between years and shift within a single non-breeding season, promoting extensive movements of birds that rely on these habitats (Roshier et al. 2002). The suitability of grasslands in semi-arid regions varies from year to year due to the differences in rainfall level. Little is known about the composition of the food resources used by waders in these inland environments, but it seems likely that these may be similar on broad spatial scales. I thus predict that coastal habitats should be more favourable to species diversification than inland habitats.

Many of the wader species that utilise coastal or inland habitats for the greater part of the year migrate to very different habitats, such Arctic tundras or boreal swamps,
breed. Whilst the reasons for this are beyond the scope of this study (but see Piersma 1997), it means that in these species reproduction is spatially separated from the feeding habitat to which they are adapted. Red knot Calidris canutus illustrate this point. For 10 months of the year, this species feeds on bivalves on mudflats around the world. The species has evolved a range of adaptations to feeding on bivalves, including a muscular stomach and sensitive bill tip (Piersma et al. 1993b, 1998). Nevertheless, it breeds exclusively on high Arctic tundras where feeding on abundant insect larvae and berries require few special adaptations. In such cases, local adaptation to, for example, temperate or tropical inter-tidal mudflats requires that birds from the same non-breeding area mate assortatively on the breeding grounds (Webster et al. 2002).

Investigating ecological speciation in this group of birds thus adds two new dimensions to the general pattern found by Funk et al. (2006) and Phillimore et al. (2007). First, as argued above, I have a priori reasons to expect that one type of habitat (coastal) should be more conducive to speciation than the other (inland). Second, many of the species investigated reproduce away from the feeding grounds to which they are adapted and speciation thus requires differential migration to achieve assortative mating. To test these ideas, I use the number of sub-species per species as a measure of diversification. Thus, I treat sub-species as ‘incipient species’. Morphological sub-species are considered useful in estimating the patterns of divergence among populations (Phillimore et al. 2007). Evidence that wader sub-species represent phylogenetically distinct groups is available for Dunlin Calidris alpina (Wenink et al. 1993), and to a lesser extent, for Red knot (Buehler and Baker 2005). Because older species could have differentiated into more sub-species than younger species, I investigated whether the number of sub-species was correlated to species age.

Materials and methods

Data collection

I collated data on the number of sub-species, migratoriness, breeding and non-breeding habitat from Del Hoyo et al. (1996) for all 215 species of the sub-order Charadrii (see Table 2 of S1). Crude estimates of species age were obtained from Thomas et al. (2004). Due to high levels of polytomy in parts of the phylogeny, some of these are likely to be over-estimates; however, no better estimates are available at present. I adopted the number of sub-species from one reputable source rather than search for the more recent updates because some of these revisions are still controversial. Migratoriness was scored as non-migrant, partial migrant or migrant (>80%, between 20% and 80% and <20% of non-breeding range overlaps with breeding range, respectively). Breeding habitat was scored as one of seven classes: tundra, boreal/temperate, mountains, steppe, (sub)tropical wetlands (either inland or coastal), (sub) tropical forest or oceanic. Non-breeding habitat was scored as coastal, inland or pelagic. For species that regularly use both coastal and inland habitats, I scored the habitat considered by Del Hoyo et al. (1996) to be used by the largest part of the population.

Statistical analysis

I first investigated whether the dependent variable (number of sub-species) showed phylogenetic auto-correlation (i.e. whether closely related species resembled each other more in their tendency to form sub-species than expected by chance) using the phylogenetic topology from Thomas et al. (2004). I used runs test as implemented in the programme Phylogenetic Independence (Abouheif 1999) to compare the observed pattern to that generated by randomly redistributing the data over the tips of the phylogeny 1,000 times. For this analysis, the number of sub-species per species was dichotomised as 1 (i.e. only the nominate form) or >1. Finding no evidence for phylogenetic autocorrelation (see the “Results” section), I treated species as independent data points in further analysis.

As the number of sub-species per species followed a Poisson distribution, I analysed the data using generalised linear models with a Poisson error distribution and a log link function. GLMStat (Beath 2001) was used to generate glms. Significance was tested by dropping each term from the fuller model and comparing the resulting change in deviance to a chi-square distribution.

Results

The results of runs test showed that there was no evidence for auto-correlation in the phylogenetic distribution of the number of sub-species (runs test \( P=0.46 \)). In fact, 461 of the 1,000 randomly generated runs averages were greater than that of the real data set, indicating a non-significant tendency towards over-dispersion.

A glm containing migratoriness, non-breeding habitat, breeding habitat and species age and their interactions showed no significant effects of three- and four-way interactions. However, there was a significant two-way interaction between migratoriness and non-breeding habitat (Table 1), indicating that the pattern of covariance between non-breeding habitat and sub-species richness differed between migrants and non-migrants. Individual models revealed a significant effect of non-breeding habitat on the
number of sub-species in migrants, but not in non-migrants or partial migrants (Table 1). These results are illustrated in Fig. 1: species wintering coastally are on average sub-divided into more sub-species than inland wintering species, but only in migrants. The results are not confounded by differences in species age (Table 1). Whilst there was a significant association between breeding and non-breeding habitat among migrants ($\chi^2 = 20.45, P=0.009$), this did not result in an association between breeding habitat and the number of sub-species (Table 1).

**Discussion**

The prediction that coastal habitats should be more conducive to diversification in waders than freshwater habitats is supported, but only for migratory species. This is remarkable, given that the reduction in gene flow between locally adapting populations requires an extra step in these species. In non-migrants, all that is needed to mate with a locally adapted partner is not to disperse. In migrants, however, all individuals migrate away from the non-breeding grounds to breed, often to the other end of the globe. To mate with a partner from the same non-breeding grounds, the non-breeding populations must either have segregated breeding grounds or have a very sophisticated individual recognition system. There is good evidence for a number of coastally wintering migrants that the former is true (Wennerberg 2001; Atkinson et al. 2005; Buehler et al. 2006), whilst the latter has not been investigated.

I suggest that the predictability of coastal non-breeding grounds favours rigid migratory pathways to and from the non-breeding grounds. Returning to the same non-breeding ground each year would save individuals from wasting time on searching for suitable non-breeding areas and allow them to benefit from learned aspects of local conditions (such as food distribution). The rigidity of the migratory pathways could then result in spatial segregation on the breeding grounds because individuals would be genetically predisposed to favour the same breeding grounds each year. The formation of distinct sub-species would then be a by-product of the spatially discontinuous distribution of non-breeding grounds. By contrast, many of the species that spend the non-breeding season on inland habitats have to track spatially and temporally variable resources (Roshier et al. 2001, 2002), which should select for flexible movement patterns during the non-breeding season. This could translate into flexible migration patterns, perhaps through a genetic correlation between migratory and non-migratory movements, and flexible movement patterns on the breeding grounds. If true, this would promote gene flow and inhibit diversification.

Alternatively, the divergent ecology of different coastal non-breeding grounds may actively select for assortative mating of corresponding ecomorphs. For example, it may be costly for waders wintering on tropical mudflats to pair with

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**Table 1** Results of the generalised linear model with the number of sub-species per species as independent variable

|                          | Estimate±SE | Deviance (df=1) | P value |
|--------------------------|-------------|-----------------|---------|
| **Minimal adequate model** |             |                 |         |
| Migratoriness            | −0.10±0.08  | 0.23            |         |
| Non-breeding habitat     | −0.16±0.19  | 0.39            |         |
| Breeding habitat         | 0.06±0.04   | 0.17            |         |
| Species age              | −0.01±0.007 | 0.11            |         |
| Migratoriness×non-breeding habitat | 0.27±0.12 | 4.92            | 0.03    |
| **Separate models**       |             |                 |         |
| Non-breeding habitat     |             |                 |         |
| Migrants                 | 0.42±0.15   | 7.39            | 0.007   |
| Partial migrants         | 0.13±0.10   | 0.07            | 0.79    |
| Non-migrants             | −0.21±0.21  | 1.07            | 0.30    |

Non-significant interaction terms were removed. P values for the main effects were obtained by using the parameter estimate divided by its standard error as the test statistic. Also shown are the results of separate models for each category of migratoriness.

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**Fig. 1** Mean number of sub-species per species for migratory and non-migratory waders. Pelagic wintering species (N=2) and partial migrants (N=31) not shown. Error bars represent the Poisson standard errors.
those that winter on temperate mudflats because the resultant hybrids would be poorly adapted to either habitat. Support for this interpretation comes from the fact that many sub-species of coastal waders differ from each other in bill length, which is an ecologically relevant trait (Engelmoer and Roselaar 1998). By contrast, the unpredictability of inland wetlands would not allow specialisation to the specific conditions presented by any particular area of habitat.

The question remains why the difference in diversification between species occupying coastal and inland habitats is not reflected in the non-migratory species that breed there? Given that migrant species often greatly outnumber resident species at individual feeding areas during the non-breeding season, migrant species may have greater effective population sizes per non-breeding area than non-migrants. This would allow more efficient response to selection and increase the potential for local adaptive change in migrants relative to non-migrants. Given the arguments above, such change is most likely in coastal areas.

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**S1. Appendix**

| Table 2  | Data used in the analysis |
|----------|---------------------------|
| **Genus** | **Species** | **Migratory** | **Winter** | **Summer** | **Sub-species** | **Species age** |
| Actitis   | hypoleucos | Migrant | Inland | Boreal | 1 | 5.779 |
| Actitis   | macularia | Migrant | Inland | Boreal | 1 | 5.779 |
| Actophilornis | africanus | Non-migrant | Inland | (Sub)tropical wetland | 1 | 8.547 |
| Actophilornis | albinucha | Non-migrant | Inland | (Sub)tropical wetland | 1 | 8.547 |
| Anarrhynchus | frontalis | Migrant | Coastal | Boreal | 1 | 26.7 |
| Aphriza   | virgata  | Migrant | Coastal | Mountain | 1 | 6.019 |
| Arenaria  | interpres | Migrant | Coastal | Tundra | 2 | 5.68 |
| Arenaria  | melanocephala | Migrant | Coastal | Tundra | 1 | 5.68 |
| Attasig   | gayi     | Non-migrant | Inland | Mountain | 3 | 18.2 |
| Attasig   | malouinus | Non-migrant | Inland | Mountain | 1 | 18.2 |
| Bartramia | longicauda | Migrant | Inland | Steppe | 1 | 20.299 |
| Burhinus  | bistriatus | Non-migrant | Inland | Steppe | 4 | 7.933 |
| Burhinus  | capensis  | Non-migrant | Inland | Steppe | 4 | 3.967 |
| Burhinus  | grallarius | Non-migrant | Inland | Steppe | 1 | 6.287 |
| Burhinus  | oedencilenus | Partial migrant | Inland | Steppe | 6 | 3.967 |
| Burhinus  | senegalensis | Non-migrant | Inland | (Sub)tropical wetland | 1 | 3.967 |
| Burhinus  | superciliaris | Non-migrant | Inland | Steppe | 1 | 11.9 |
| Burhinus  | vermiculatus | Non-migrant | Inland | (Sub)tropical wetland | 2 | 19.8 |
| Calidris  | acuminata | Migrant | Inland | Tundra | 1 | 3.798 |
| Calidris  | alba      | Migrant | Coastal | Tundra | 1 | 8.707 |
| Calidris  | alpina    | Migrant | Coastal | Tundra | 9 | 7.836 |
| Calidris  | bairdii   | Migrant | Inland | Tundra | 1 | 7.4 |
| Calidris  | canutus   | Migrant | Coastal | Tundra | 5 | 3.798 |
| Calidris  | ferruginea | Migrant | Coastal | Tundra | 1 | 17.413 |
| Calidris  | fuscicollis | Migrant | Coastal | Tundra | 1 | 6.965 |
| Calidris  | maritima  | Partial migrant | Coastal | Tundra | 1 | 2.588 |
| Calidris  | mauri     | Migrant | Coastal | Tundra | 1 | 9.142 |
| Calidris  | melanotos | Migrant | Inland | Tundra | 1 | 4.136 |
| Calidris  | minuta    | Migrant | Coastal | Tundra | 1 | 3.483 |
| Calidris  | minuilla  | Migrant | Inland | Boreal | 1 | 6.965 |
| Calidris  | pitocnemis | Partial migrant | Coastal | Tundra | 4 | 2.588 |
| Calidris  | pusilla   | Migrant | Coastal | Tundra | 1 | 3.483 |
| Calidris  | ruficollis | Migrant | Coastal | Tundra | 1 | 2.609 |
| Calidris  | subminuta | Migrant | Inland | Boreal | 1 | 2.609 |
| Calidris  | temminckii | Migrant | Inland | Boreal | 1 | 10.013 |
Table 2 (continued)

| Genus          | Species         | Migratory | Winter          | Summer          | Sub-species | Species age |
|----------------|-----------------|-----------|-----------------|-----------------|-------------|-------------|
| Calidris       | tenuirostris    | Migrant   | Coastal Mountain | Steppe          | 1           | 3.798       |
| Charadrius     | alexandrinus    | Partial migratory | Coastal (Sub)tropical wetland | 5 | 22.992 |
| Charadrius     | aliticola       | Non-migrant | Inland Mountain | Steppe          | 1           | 22.992      |
| Charadrius     | asiaticus       | Migrant  | Inland Steppe   | Boreal          | 2           | 7.224       |
| Charadrius     | bicinctus       | Partial migratory | Coastal Boreal  | 1             | 22.992      |
| Charadrius     | collaris        | Non-migrant | Inland (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | dubius          | Partial migratory | Inland (Sub)tropical wetland | 3 | 12.882 |
| Charadrius     | falklandicus    | Partial migratory | Coastal Boreal  | 1             | 16.317      |
| Charadrius     | forbesi         | Partial migratory | Inland Steppe   | 1             | 22.992      |
| Charadrius     | hiaticula       | Migrant   | Coastal Tundra  | 2              | 8.793       |
| Charadrius     | javanicus       | Non-migrant | Coastal (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | leschenaultii   | Migrant  | Coastal Steppe  | 3              | 22.992      |
| Charadrius     | marginatus      | Non-migrant | Coastal (Sub)tropical wetland | 4 | 22.992 |
| Charadrius     | melodus         | Migrant   | Coastal (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | modestus        | Partial migratory | Inland Boreal   | 1             | 19.283      |
| Charadrius     | mongolus        | Migrant   | Coastal Mountain | 5             | 7.224       |
| Charadrius     | montanus        | Migrant   | Inland Steppe   | 1              | 16.317      |
| Charadrius     | morinellus      | Migrant   | Inland Tundra   | 1              | 26.7        |
| Charadrius     | novaseelandi    | Non-migrant | Coastal Oceanic island | 1 | 4.558       |
| Charadrius     | obscursus       | Partial migratory | Coastal Boreal  | 2             | 22.992      |
| Charadrius     | pallidus        | Non-migrant | Inland (Sub)tropical wetland | 2 | 22.992 |
| Charadrius     | pecuarius       | Non-migrant | Inland (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | peronii         | Non-migrant | Coastal (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | placidus        | Migrant   | Inland (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | rufigollis      | Non-migrant | Coastal (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | sanctaehelena   | Non-migrant | Inland Oceanic island | 1 | 22.992 |
| Charadrius     | semipalmaus     | Migrant   | Coastal Tundra  | 1              | 11.096      |
| Charadrius     | thoracicus      | Non-migrant | Coastal (Sub)tropical wetland | 1 | 22.992 |
| Charadrius     | tricoloris      | Non-migrant | Inland (Sub)tropical wetland | 2 | 5.548 |
| Charadrius     | veredus         | Migrant   | Inland Steppe   | 1              | 7.224       |
| Charadrius     | vociferus       | Partial migratory | Inland (Sub)tropical wetland | 3 | 5.548 |
| Charadrius     | wilsonia        | Partial migratory | Coastal (Sub)tropical wetland | 3 | 5.548 |
| Chionis        | alba            | Partial migratory | Coastal Oceanic island | 1 | 11.988 |
| Chionis        | minor           | Non-migrant | Coastal Oceanic island | 4 | 11.988 |
| Cladorhynchus  | leucocephalus   | Partial migratory | Inland (Sub)tropical wetland | 1 | 10.182 |
| Coenocorypha   | aucklandica     | Non-migrant | Inland Oceanic island | 4 | 4.91 |
| Coenocorypha   | pusilla         | Non-migrant | Inland Oceanic island | 1 | 4.91 |
| Cursorius      | coromandeliciu  | Non-migrant | Inland Steppe   | 1              | 9.9         |
| Cursorius      | cursor          | Partial migratory | Inland Steppe   | 5             | 4.95        |
| Cursorius      | rufus           | Non-migrant | Inland Steppe   | 1              | 4.95        |
| Cursorius      | temminckii      | Partial migratory | Inland Steppe   | 1              | 9.9         |
| Elseornis      | melanops        | Non-migrant | Inland (Sub)tropical wetland | 1 | 22.992 |
| Erythrogonys   | cinctus         | Non-migrant | Inland (Sub)tropical wetland | 1 | 23.256 |
| Esacus         | magirosthis     | Non-migrant | Coastal (Sub)tropical wetland | 1 | 3.967 |
| Esacus         | recurvirostrois | Non-migrant | Inland (Sub)tropical wetland | 1 | 9.21 |
| Euryorhynchus  | pygmeus         | Migrant   | Coastal Tundra  | 1              | 17.413      |
| Gallinago      | gallinago       | Migrant   | Inland Boreal   | 3              | 19.576      |
| Gallinago      | hardwickii      | Migrant   | Inland Boreal   | 1              | 19.576      |
| Gallinago      | imperialis      | Non-migrant | Inland Mountain | 1             | 19.576      |
| Gallinago      | jamesonii       | Non-migrant | Inland Mountain | 1             | 19.576      |
| Gallinago      | macroactyla     | Non-migrant | Inland (Sub)tropical wetland | 1 | 4.894 |
| Gallinago      | media           | Migrant   | Inland Boreal   | 1              | 4.894       |
| Gallinago      | megalus         | Migrant   | Inland Boreal   | 1              | 4.894       |
| Gallinago      | nemoricola      | Partial migratory | Inland Mountain | 1             | 19.576      |
Table 2 (continued)

| Genus       | Species                  | Migratory | Winter          | Summer          | Sub-species | Species age |
|-------------|--------------------------|-----------|-----------------|-----------------|-------------|-------------|
| Gallinago   | nigripennis              | Non-migrant | Inland | Mountain | 3 | 4.894 |
| Gallinago   | nobilis                  | Non-migrant | Inland | Mountain | 1 | 19.576 |
| Gallinago   | paraguaiae               | Non-migrant | Inland | (Sub)tropical wetland | 3 | 19.576 |
| Gallinago   | solitaria                | Partial migrant | Inland | Mountain | 2 | 19.576 |
| Gallinago   | stenura                  | migrant | Inland | Boreal | 1 | 19.576 |
| Gallinago   | stricklandii             | Non-migrant | Inland | Boreal | 1 | 19.576 |
| Gallinago   | undulata                 | Non-migrant | Inland | (Sub)tropical wetland | 2 | 19.576 |
| Glareola    | cinerea                  | Non-migrant | Inland | (Sub)tropical wetland | 1 | 13.896 |
| Glareola    | lactea                   | Partial migrant | Inland | (Sub)tropical wetland | 1 | 13.896 |
| Glareola    | maldivarum               | Migrant | Inland | Steppe | 1 | 13.896 |
| Glareola    | nordmanni                | Migrant | Inland | Steppe | 1 | 13.896 |
| Glareola    | nuchalis                 | Non-migrant | Inland | (Sub)tropical wetland | 2 | 13.896 |
| Glareola    | ocularis                 | Migrant | Inland | (Sub)tropical wetland | 1 | 13.896 |
| Glareola    | praticola                | Migrant | Inland | (Sub)tropical wetland | 3 | 13.896 |
| Haematopus  | ater                     | Non-migrant | Coastal | Boreal | 1 | 4.283 |
| Haematopus  | bachmani                 | Non-migrant | Coastal | Boreal | 1 | 4.283 |
| Haematopus  | chathamensis             | Non-migrant | Coastal | Oceanic island | 1 | 6.789 |
| Haematopus  | fuliginosus              | Non-migrant | Coastal | (Sub)tropical wetland | 2 | 12.849 |
| Haematopus  | leucopodus               | Non-migrant | Coastal | Boreal | 1 | 14.817 |
| Haematopus  | longirostris             | Non-migrant | Coastal | (Sub)tropical wetland | 1 | 14.817 |
| Haematopus  | meadewaldoi              | Non-migrant | Coastal | Oceanic island | 1 | 14.817 |
| Haematopus  | moquini                  | Non-migrant | Coastal | Boreal | 1 | 11.072 |
| Haematopus  | ostralegus               | Migrant | Coastal | Boreal | 4 | 4.283 |
| Haematopus  | palliatus                | Non-migrant | Coastal | (Sub)tropical wetland | 2 | 12.024 |
| Haematopus  | unicolor                 | Non-migrant | Coastal | Boreal | 1 | 4.283 |
| Heteroscelus| brevispes                | Migrant | Coastal | Mountain | 1 | 5.324 |
| Heteroscelus| incanus                  | Migrant | Coastal | Mountain | 1 | 5.324 |
| Himantopus  | himantopus               | Partial migrant | Inland | (Sub)tropical wetland | 5 | 8.77 |
| Himantopus  | novaezelandia            | Non-migrant | Coastal | Boreal | 1 | 8.77 |
| Hydrophasianus| chirurgus              | Partial migrant | Inland | (Sub)tropical wetland | 1 | 17.118 |
| Ibidorhyncha| struthersii             | Non-migrant | Inland | Mountain | 1 | 16.5 |
| Irediparra  | gallinacea               | Non-migrant | Inland | (Sub)tropical wetland | 3 | 8.547 |
| Jacana      | jacana                   | Non-migrant | Inland | (Sub)tropical wetland | 6 | 10.8 |
| Jacana      | spinosa                  | Non-migrant | Inland | (Sub)tropical wetland | 3 | 10.8 |
| Limicola    | falcinellus              | Migrant | Coastal | Tundra | 2 | 3.798 |
| Limnodromus | griseus                  | Migrant | Coastal | Boreal | 3 | 4.951 |
| Limnodromus | scolopaceus              | Migrant | Inland | Tundra | 1 | 4.951 |
| Limnodromus | semipalatus              | Migrant | Coastal | Boreal | 1 | 7.847 |
| Limosa      | fedoa                    | Migrant | Coastal | Steppe | 2 | 11.739 |
| Limosa      | haemastica               | Migrant | Coastal | Tundra | 1 | 9.303 |
| Limosa      | lapponica                | Migrant | Coastal | Tundra | 3 | 5.869 |
| Limosa      | limosa                   | Migrant | Coastal | Steppe | 3 | 5.869 |
| Lymnocryptes| minimus                  | Migrant | Inland | Boreal | 1 | 21.8 |
| Metopidius  | indicus                  | Non-migrant | Inland | (Sub)tropical wetland | 1 | 13.546 |
| Micropalama | himantopus               | Migrant | Inland | Tundra | 1 | 17.413 |
| Microparra  | capensis                 | Non-migrant | Inland | (Sub)tropical wetland | 1 | 8.547 |
| Numenius    | americanus               | Migrant | Inland | Steppe | 2 | 6.404 |
| Numenius    | arquata                  | Migrant | Coastal | Boreal | 2 | 6.404 |
| Numenius    | borealis                 | Migrant | Inland | Tundra | 1 | 19.211 |
| Numenius    | madagascarien           | Migrant | Coastal | Boreal | 1 | 6.404 |
| Numenius    | minutus                  | Migrant | Inland | Boreal | 1 | 19.211 |
| Numenius    | phaeopus                 | Migrant | Coastal | Boreal | 4 | 10.15 |
| Numenius    | tahitiensis              | Migrant | Coastal | Tundra | 1 | 6.404 |
| Numenius    | tenuirostris            | Migrant | Inland | Boreal | 1 | 19.211 |
| Oreopholus  | ruficollis               | Partial migrant | Inland | Mountain | 2 | 30.733 |
| Pedionomus  | torquatus                | Non-migrant | Inland | Steppe | 1 | 45.8 |
| Genus      | Species         | Migratory | Winter       | Summer       | Sub-species | Species age |
|------------|-----------------|-----------|--------------|--------------|-------------|-------------|
| Peltohyas  | australis       | Non-migrant | Inland      | Steppe       | 1           | 4.558       |
| Phalaropus | fulicaria       | Migrant   | Pelagic      | Tundra       | 1           | 2.158       |
| Phalaropus | lobatus         | Migrant   | Pelagic      | Tundra       | 1           | 2.158       |
| Phegornis  | mitchelli       | Non-migrant | Inland      | Mountain     | 1           | 26.7        |
| Philomachus| pugnax          | Migrant   | Inland      | Tundra       | 1           | 6.019       |
| Pluvialis  | apricaria       | Migrant   | Inland      | Tundra       | 2           | 8.33        |
| Pluvialis  | dominica        | Migrant   | Inland      | Tundra       | 1           | 5.256       |
| Pluvialis  | fulva           | Migrant   | Coastal     | Tundra       | 1           | 5.256       |
| Pluvialis  | squatarola      | Migrant   | Coastal     | Tundra       | 1           | 10.511      |
| Pluvianellus| socialis     | Partial migrant | Coastal    | Boreal       | 1           | 19          |
| Pluvianus  | aegyptius       | Non-migrant | Inland      | (Sub)tropical wetland | 1 | 36.9       |
| Prosobonia | cancellata      | Non-migrant | Coastal    | Oceanic island | 1 | 5.517       |
| Recurvirostra | americana  | Migrant | Inland      | Boreal       | 1           | 4.385       |
| Recurvirostra | andina      | Non-migrant | Inland     | Mountain     | 1           | 4.385       |
| Recurvirostra | avosetta    | Partial migrant | Inland     | (Sub)tropical wetland | 1 | 8.77        |
| Recurvirostra | novaehollandi | Partial migrant | Inland     | (Sub)tropical wetland | 1 | 6.95        |
| Rhinoptilus | africanus      | Non-migrant | Inland     | Steppe       | 8           | 9.9         |
| Rhinoptilus | bitorquatus     | Non-migrant | Inland     | Steppe       | 1           | 7.846       |
| Rhinoptilus | chalcopertus    | Partial migrant | Inland     | Steppe       | 1           | 4.95        |
| Rhinoptilus | cinctus        | Non-migrant | Inland     | Steppe       | 3           | 4.95        |
| Rostratula | bengaleensis    | Non-migrant | Inland     | (Sub)tropical wetland | 2 | 27.5        |
| Rostratula | semicollaris    | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 27.5        |
| Scolopax  | celebensis      | Non-migrant | Inland     | (Sub)tropical forest | 1 | 12.057      |
| Scolopax  | minor           | Partial migrant | Inland     | (Sub)tropical forest | 1 | 12.057      |
| Scolopax  | mira            | Non-migrant | Inland     | (Sub)tropical forest | 1 | 4.664       |
| Scolopax  | rochussenii     | Non-migrant | Inland     | (Sub)tropical forest | 1 | 12.057      |
| Scolopax  | rusticola       | Migrant   | Inland     | Boreal       | 1           | 4.664       |
| Scolopax  | saturata        | Non-migrant | Inland     | (Sub)tropical forest | 2 | 12.057      |
| Steganopus | tricolor        | Migrant   | Inland     | Steppe       | 1           | 3.42        |
| Stiltia  | isabella        | Partial migrant | Inland     | Steppe       | 1           | 14.85       |
| Thinocorus | orbignianus     | Non-migrant | Inland     | Mountain     | 2           | 19.352      |
| Thinocorus | rumicivorus     | Partial migrant | Inland     | Mountain     | 4           | 19.352      |
| Tringa    | erythropus      | Migrant   | Inland     | Tundra       | 1           | 5.324       |
| Tringa    | flavipes        | Migrant   | Inland     | Boreal       | 1           | 13.762      |
| Tringa    | glareola        | Migrant   | Inland     | Boreal       | 1           | 8.438       |
| Tringa    | guttifer        | Migrant   | Coastal    | Boreal       | 1           | 19.086      |
| Tringa    | melanoleuca     | Migrant   | Inland     | Boreal       | 1           | 5.324       |
| Tringa    | nebularia       | Migrant   | Inland     | Boreal       | 1           | 13.762      |
| Tringa    | ochropus        | Migrant   | Inland     | Boreal       | 1           | 19.086      |
| Tringa    | solitaria       | Migrant   | Inland     | Boreal       | 2           | 19.086      |
| Tringa    | stagnatilis     | Migrant   | Inland     | Boreal       | 1           | 13.762      |
| Tringa    | totanus         | Migrant   | Coastal    | Boreal       | 6           | 13.762      |
| Tringites | subruficollis   | Migrant   | Inland     | Tundra       | 1           | 10.448      |
| Vanellus  | albiceps        | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 22.961      |
| Vanellus  | armatus         | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 5.008       |
| Vanellus  | cayanus         | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 22.961      |
| Vanellus  | chilensis       | Non-migrant | Inland     | (Sub)tropical wetland | 4 | 5.008       |
| Vanellus  | cinereus        | Migrant   | Inland     | (Sub)tropical wetland | 1 | 22.961      |
| Vanellus  | coronatus       | Non-migrant | Inland     | Steppe       | 2           | 22.961      |
| Vanellus  | crassirostris   | Non-migrant | Inland     | (Sub)tropical wetland | 2 | 5.008       |
| Vanellus  | duvaucelii      | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 7.937       |
| Vanellus  | gregarius       | Migrant   | Inland     | Steppe       | 1           | 5.008       |
| Vanellus  | indicus         | Non-migrant | Inland     | (Sub)tropical wetland | 4 | 5.008       |
| Vanellus  | leucurus        | Partial migrant | Inland     | (Sub)tropical wetland | 1 | 22.961      |
| Vanellus  | lugubris        | Non-migrant | Inland     | Steppe       | 1           | 5.008       |
| Vanellus  | macropterus     | Non-migrant | Inland     | (Sub)tropical wetland | 1 | 5.008       |
Table 2 (continued)

| Genus  | Species       | Migratory | Winter       | Summer       | Sub-species | Species age |
|--------|---------------|-----------|--------------|--------------|-------------|-------------|
| Vanellus | malabaricus  | Non-migrant | Inland      | Steppe       | 1           | 22.961      |
| Vanellus | melanopeplus  | Non-migrant | Inland      | Mountain     | 1           | 22.961      |
| Vanellus | miles         | Non-migrant | Inland      | Steppe       | 2           | 22.961      |
| Vanellus | resplendens   | Non-migrant | Inland      | Mountain     | 1           | 5.008       |
| Vanellus | senegalensis  | Non-migrant | Inland      | (Sub)tropical wetland | 3 | 22.961      |
| Vanellus | spinosus      | Non-migrant | Inland      | (Sub)tropical wetland | 1 | 5.008       |
| Vanellus | superciliosus | Migrant    | Inland      | Steppe       | 1           | 22.961      |
| Vanellus | tectus        | Non-migrant | Inland      | Steppe       | 2           | 5.008       |
| Vanellus | tricolor      | Non-migrant | Inland      | Steppe       | 1           | 5.008       |
| Vanellus | vanellus      | Migrant    | Inland      | Steppe       | 1           | 22.961      |
| Xenus   | cinereus      | Migrant    | Coastal     | Boreal       | 1           | 32.1        |

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