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Territoriality and density of an Australian migrant, the Buff-breasted Paradise Kingfisher, in the New Guinean non-breeding grounds

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Abstract. We report on the non-breeding dispersion and density of Buff-breasted Paradise Kingfishers (*Tanysiptera syliva sylvia*), an Australo-Papuan intratropical migrant. The study was carried out at the base of the Hunstein Range, in the Sepik basin of Papua New Guinea, using playbacks of calls to census for the presence of birds. Preliminary density estimates (0.4–1.0 birds ha^{-1}) were higher than expected on the basis of the paucity of museum specimens, the results of broad-scale bird surveys, and observational records. This difference is probably due to their extremely shy behaviour, which would cause them to be under-represented using standard survey methods. Most importantly, at least some kingfishers were territorial, with just a single bird defending each territory. Birds responded to playbacks of their calls using stereotypical territorial responses, and attacked models vigorously. These observations suggest that kingfishers compete for resources at their non-breeding grounds. At least in this species, competition during the non-breeding season may therefore have been a factor in the evolution of intratropical migration, as suggested for the better-studied temperate–tropical migrant species of North America and Europe. In addition, if demographic processes during the non-breeding season are found to limit populations in other Australo-Papuan migrants, the impending massive habitat loss in the Australasian and south-east Asian tropics may have devastating effects on many of these species.

Introduction

The study of bird migration has a relatively long history (Berthold 1993). Despite this, it has suffered from a glaring issue of biased perspective. Research into all aspects of migration has been dominated by biologists working in the temperate regions of Europe and North America. Until the 1980s, the standard paradigm of migration has therefore been that birds breed at temperate latitudes during the summer (when resources are superabundant, and predation and interspecific competition are both low), but escape the harsh winter climate by migrating towards the Equator for the non-breeding season (Gauthreaux 1982).

This 'northern temperate' view has resulted in two important intellectual inertias. First, the ecological importance of several other major migration systems has been neglected, notably the Southern Hemisphere migrations (South American and Australasian), and the intratropical migrations. The scale, species' distributional patterns, and ecological correlates of these alternative migration systems are only just beginning to be examined (e.g. Chesser 1998; Hockey 2000). Second, by concentrating on ecological and demographic processes at the breeding grounds, the northern temperate bias ignored the significance of competition in tropical communities as an evolutionarily important force in migrant biology (Keast 1980). Recent studies of the ecology of migrants in their non-breeding range are starting to redress this imbalance (Keast and Morton 1980; Martin and Finch 1995). Despite these promising developments, it is still the case that the overwhelming bulk of ecological and demographic data on migrant birds are confined to the breeding seasons of the northern temperate zone. Information from the non-breeding stages is relatively rare, and almost exclusively confined to birds of the temperate–tropical migration systems.

The study of landbird migration in Australasia has lagged far behind Europe and North America partly because the area's small and patchily distributed human population makes collection of even basic distributional data difficult. Descriptive information about which species migrate, and where they go, has improved in the last three decades, with a small number of detailed studies on single species or species groups (e.g. Keast 1968; Wyndham 1982; Bell and Ford 1987; Chan and Kikkawa 1997; Mac Nally and Horrocks 2000), and various compilations that document migratory behaviour across species (e.g. Draffan *et al*. 1983; Fullagar *et al*. 1988; Chan 2001). These compilations have shown that a large proportion of breeding landbirds in Australasia migrate (40%: Chan 2001). Most are intracontinental, but the Torres Strait acts as a conduit for many species *en route* to non-breeding grounds in New Guinea and south-east Asia (Draffan *et al*. 1983).

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In a remarkable set of models, Nix (1976) used climatic information and ecological data to predict the direction of movements for different foraging guilds in Australia and New Guinea. However, our understanding of the ecological basis of Australasian migration has advanced little since this pioneering work, and we still know next to nothing about the ecological requirements and demographic processes affecting populations at different stages of their migration, particularly for those species that cross the Torres Strait. Such knowledge is vital for a better understanding of Australasian migration, as well as the effective conservation of migrants (Chan 2001).

The Australian sub-species of the Buff-breasted Paradise Kingfisher (*Tanysiptera sylvia sylvia*) breeds in Queensland's lowland tropical rainforests between Mackay and Cape York during the wet season (November–April), and migrates to New Guinea for the non-breeding season (Legge and Heinsohn 2001). Depending on the precise breeding and non-breeding destinations, the migration distance for each population may vary from 400 to 2000 km. The non-breeding distributional limits are unclear: the bird is rarely seen by birdwatchers and naturalists, and just 12 specimens have been collected during museum expeditions to New Guinea. These have come from both the lowland basins to the north and south of the central cordillera, as far west as the Setekwa River in West Papua, Indonesia; it has also been recorded as far east as the Lakekamu basin in the Gulf Province of Papua New Guinea (Beehler *et al*. 1995; Beehler and Mack 1999) (Fig. 1). Depending on the classification, up to three other subspecies are recognised: *T. s. leucura* on Umboi Island, *T. s. nigriceps* on New Britain, and *T. s. salvadoriana* near Port Moresby (del Hoyo *et al*. 2001). These three taxa are sedentary, and allopatric with the migratory subspecies while it is in New Guinea (Fig. 1).

The breeding biology, social and spacing systems, and survival of the Buff-breasted Paradise Kingfisher while it is in Australia are relatively well described (Legge and Heinsohn 2001). However, nothing is known of its social system, survival, movement patterns and habitat requirements during the non-breeding season. In this study, we report on the density and dispersion system of the Buff-breasted Paradise Kingfisher in the Sepik region of Papua New Guinea. To our knowledge this is the first report of the non-breeding dispersion system for an Australo-Papuan migrant, and one of the few (if not the first) report of the non-breeding dispersion of an intratropical migrant worldwide.

Methods

Study area

The study was carried out from 12 to 21 June 2003 at the base of the Hunstein Range, in the Sepik River basin, East Sepik Province, Papua New Guinea (4°36′50″S, 142°42′52″E; 60 m above sea level) (Fig. 1). The study site was 4 km west of Gahom village and 2km north of the Sitipa River, a tributary of the April River (known as the Niksec by locals), which is itself a major tributary of the Sepik River.

The area receives ~4000 mm of rain each year, with June to September being relatively drier months (Shearman 1999). From the banks of the Sitipa River the topography is very flat until it reaches the Hunstein foothills. This flat area is a poorly drained, fine-textured alluvium that experiences frequent and prolonged inundation when the Sitipa is in flood. The ground is thickly layered with mud, there is very little leaf litter build-up or understorey, and the vegetation includes types of swamp forest. Even a slight rise in elevation of a few metres results in firmer ground, humus build-up, and a thicker understorey. With increasing elevation, the vegetation grades into the extremely

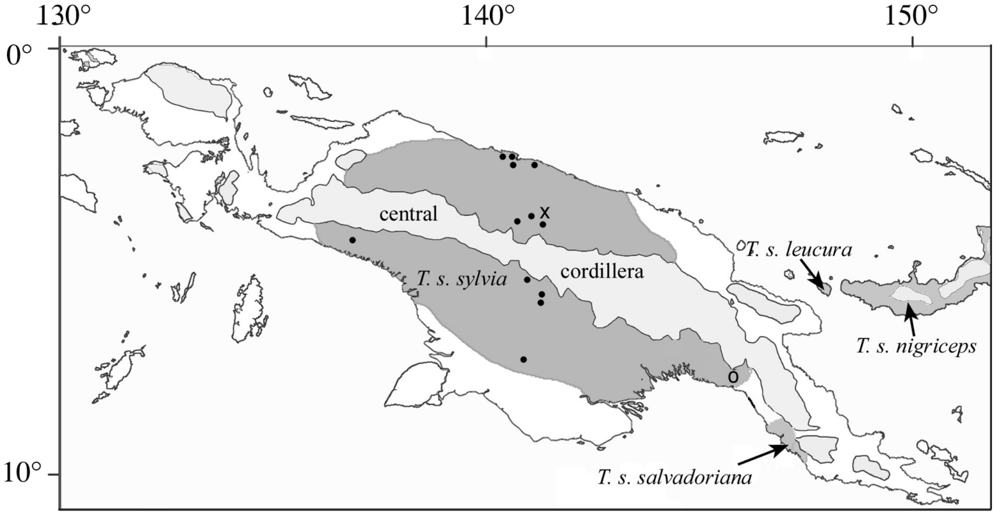

Fig. 1. Map of New Guinea showing the presumed distribution of *T. s. sylvia* as the dark grey shaded area. The collection sites of museum specimens are indicated with dots; the open circle shows additional observational records from the Lakekamu Basin that extends the known distribution eastwards. The location of our study site is marked with a cross. The distributions of the three non-migratory subspecies are also shown in mid-grey shading. Areas of high elevation are lightly shaded.

diverse hill forest of the Hunstein Ranges (Shearman 1999). In order to incorporate both types of forest structure, we carried out the surveys where the floodplain met the Hunstein foothills.

Survey methods

We used recordings of Buff-breasted Paradise Kingfisher calls to census for the presence of birds along three marked transects. Each transect followed an indistinct path made by hunters, was 620–920 m in length, and was marked every 60–100 m with flagging tape. The intervals were designed to be just less than the maximum distance at which we could hear a paradise kingfisher calling from; therefore in thicker vegetation we shortened the intervals. The transect path and position of interval points were recorded with a Garmin GPS hand-held unit.

We walked slowly along each transect, stopped at each interval point to play 20 s of pre-recorded kingfisher calls, paused for 30 s, then played 20 s of calls again. The approximate positions of birds that responded to the playbacks were plotted on a map (using Gartrip 205a) by estimating the distance and compass bearing from the census point. Once birds were prompted to respond, they called persistently for up to several minutes, rarely moving while calling (similar to their behaviour at our Australian study sites), so it was easy to keep track of the whereabouts of two or three birds calling simultaneously as we walked along the transect.

Transects were surveyed between 0700 and 0900 hours and 1700 and 1800 hours, when this species tends to be more active. To avoid habituation to playback, a transect was never resurveyed until at least one and a half days had passed since its last census. Surveys were conducted along the ‘Camp transect’ (a low ridge that rose 60 m above the floodplain) on four occasions, along the ‘Wagu transect’ (on the floodplain) on three occasions, and on two occasions along the ‘Gahom transect’ (also on the floodplain). During one survey on the Camp transect equipment failure caused us to abandon the last four playbacks, resulting in a total of 86 playbacks. Summary statistics on response rates and the density of birds were calculated for each complete survey, and then averaged for all the surveys on a particular transect.

If we were on one of the transects for other reasons and heard a bird calling unprovoked by a playback, its position was also marked on a map.

Capture methods

We attempted to catch a small number of birds in elevated mist nets (10–12 m high) by enticing them to attack a kingfisher model mounted on a tree beside the net. The body of the model had a solenoid embedded into it, which was connected to a sound-activated relay. We placed a small speaker next to the relay and robot, and connected this with 30 m of cabling to a portable tape player and a small 12-V battery, which we operated from within a hide. When we played a recording of a calling kingfisher, with every call the relay passed current to the solenoid, which lifted the tail in a flicking motion. This closely mimics the kingfisher’s territorial display during the breeding season in Australia, where perched birds tail-flick for up to several minutes in time to their calls.

Results

Territoriality

It quickly became clear that at least some birds were territorial, for several reasons. First, Buff-breasted Paradise Kingfishers responded to playbacks with a stereotypical territorial response – they perched in the upper canopy and called antiphonally with the playback for several minutes, beating their tails up and down in time with their calls, and puffing out the feathers on their backs. This is the standard display between two or more territory-holding birds while on the Australian breeding grounds (authors’ observations). Second, when presented with the robotic model, the kingfishers responded aggressively and attacked the model (this is also the standard response to model presentation in Australia). Third, birds called from the same positions during different playback surveys and at other times when they were unprovoked by playback. For example, from our campsite up to five birds could be heard calling simultaneously, each from the same positions on every occasion. At their Australian breeding grounds, birds also have a focal point in their territory from which they broadcast their territorial calls. As final confirmation of territoriality, we used the robotic model and playback to lure three kingfishers (in three different places) into mist nets. After banding two of these birds, we continued to resight them 0–40 m from their capture locations.

On every occasion that a bird called (whether unprovoked or in response to a playback) it called alone, never as part of a pair. In other words, territories were defended by a single bird, unlike in Australia where territories are defended by a pair. Both male and female individuals defended territories. Although the birds were extremely difficult to observe closely enough to identify their sex (on the basis of subtle colour differences on the back and tail streamers: Legge and Heinsohn 2001), we were able to examine the three birds that we caught using the robotic model and mist net; one was male and two were female. All had responded vocally to the playbacks and attacked the model aggressively. Note that breeding females in Australia attack models much less frequently than males, perhaps because their male partners usually perform this defensive role.

Survey results

Overall, the 86 playbacks performed during surveys elicited 37 responses. The average response rate to playback across all nine transects was 0.44 (s.d. = 0.16). Although the sample is too small for statistical comparison, the response rate did not appear to vary among transects (response rate averaged over all surveys was 0.49, 0.40, and 0.40 for the Camp, Wagu, and Gahom transects, respectively).

The observed playback response rates underestimated the true density of birds because individual birds did not respond to every playback. For example, from our camp we heard a single male calling from the same position several times a day. He also responded to some playbacks that we broadcast at random times. We caught this male with the use the robotic model, and continued to hear and see him on his territory after he was banded. His territory lay along one transect, yet he never responded to a playback that was broadcast during a formal survey. Birds seemed very sensitive to our presence and skulked away silently when they were aware of us; we suspect this was the main cause of variability in an individual’s response. By combining the results of repeated surveys on each transect, and including the positions of birds that called unprovoked by playback, we improved the estimate of the dispersion of birds along each transect. If calls were heard from two very close positions (<80 m apart) on different days, we assumed that they were made by the same bird. If calls on different days were over 80 m apart, it was difficult to know whether there were one or two birds in that area. However, in practice, birds from adjacent territories often called at the same time, confirming the existence of two rather than one larger territory.

The Camp transect, which was on slightly higher-elevation ground, had at least 13 birds distributed along its length (Fig. 2*a*). Assuming that we could hear calls up to 80 m perpendicular to the transect path, the density of birds was 1.04 birds ha^{-1}. The density on the floodplain was 0.41 birds ha^{-1} for the Wagu transect (Fig. 2*b*), and 0.45 birds ha^{-1} for the Gahom transect (Fig. 2*c*). The density of birds on the higher ground appears greater than on the floodplain transects, but this should be treated cautiously as we carried out more surveys and spent more time in general on the Camp transect, and probably detected more birds there as a consequence.

Discussion

Density

Buff-breasted Paradise Kingfishers at the study site were extremely cryptic, secretive, and relatively silent. The background calling rates were lower than during the breeding

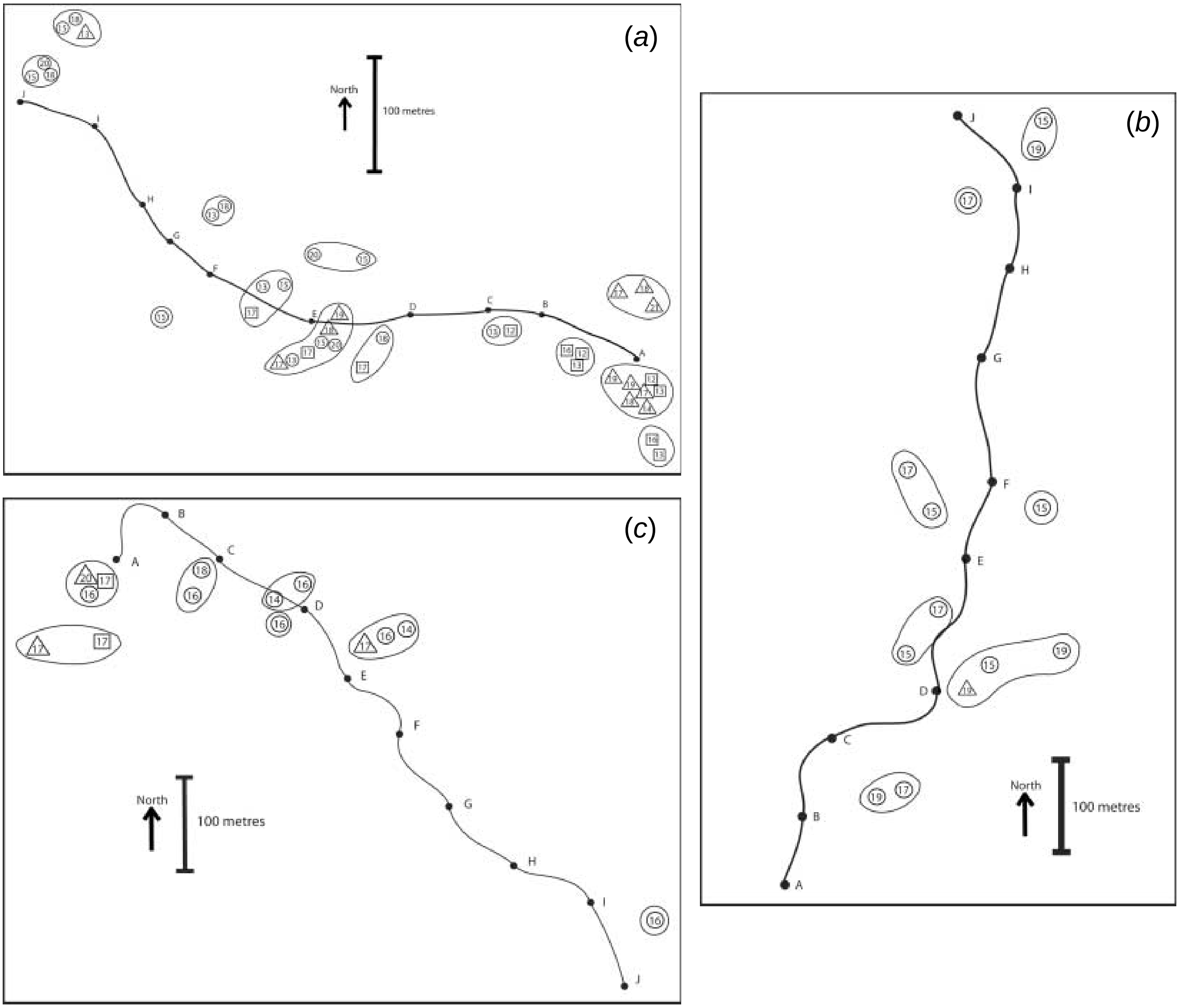

Fig. 2. The positions of birds heard along the (*a*) Camp, (*b*) Wagu and (*c*) Gahom transects, during surveys or incidentally. Letters show the position of playback locations. The numbers indicate the date the call was heard (13 = 13 June 2003, etc). Numbers in circles indicate that the call was heard in response to a playback; numbers in squares indicate that the call was unprovoked, but was heard at the same time as another bird(s) (thus confirming the existence of two or more birds in one area). Numbers in triangles indicate unprovoked calls; no other birds were calling at the same time.

season in Australia. The closely related Common Paradise Kingfisher (*T. galatea*) has also been reported to call much less frequently during the non-breeding season, even though it is sedentary and territorial all year (Bell 1980).

Buff-breasted Paradise Kingfishers are believed to be rare in New Guinea, as evidenced by the small number of specimens in museums worldwide, the few observational records (D. Bishop, D. Coates, J. Diamond, and P. Gregory, personal communications), and the low frequency with which the bird appears in general bird-survey results (e.g. Beehler *et al.* 1995; Mack and Wright 1996; Beehler and Mack 1999). Against this background, the density of kingfishers at the Gahom study site may seem unusually high. However, the kingfisher's extremely wary behaviour and infrequent calling have probably caused it to be overlooked by collectors, survey teams and birdwatchers. For example, during this study, one of us (P. Igag) conducted a broad-scale netting survey involving 220 mist-net-days without catching a single Buff-breasted Paradise Kingfisher, even though there were many birds in the vicinity. The distribution and abundance of many species of non-breeding birds, including migrants, may be difficult to assess without a tool such as playbacks to trigger a response.

The density of Buff-breasted Paradise Kingfishers reported here (0.4–1.0 birds ha^{-1}) is probably an underestimate because individual birds did not respond to every playback they heard. Because of this, and the fact that our sample of transects is small, the estimate needs to be treated with caution. Nevertheless, some comparisons with the results of other studies can be made. Our estimate falls at the lower end of the range of known densities of Buff-breasted Paradise Kingfishers in Australia, from 10 birds ha^{-1} at the Tip of Cape York (Beruldsen 1990), to 4 birds ha^{-1} at Iron Range National Park (Legge and Heinsohn 2001), down to 1 bird ha^{-1} in suitable habitat near Mackay (S. Legge, unpublished data). The only density estimate for any species of paradise kingfisher in New Guinea comes from Brown River, near Port Moresby, where the Common Paradise Kingfisher was one of the most abundant birds in the forest at 5 birds ha^{-1} (Bell 1980).

Territoriality

The key result from this study is that at least some Buff-breasted Paradise Kingfishers of both sexes maintain single-bird territories, using calls, stereotypical tail-flicking displays, and direct attacks to model 'intruders'. Since this species does not breed in New Guinea, these territories are probably defended exclusively for food resources. This differs from their social system in Australia, where pairs occupy all-purpose territories for breeding and foraging, and males defend more aggressively than females (authors' observations), probably because males are engaged in defence of both food and mates.

Of the limited information available from other tropical areas in the non-breeding season, a range of dispersion systems has been reported from strict territory defence to nomadism. Single-bird territoriality appears to be relatively common in passerines overwintering in the Neotropics (Greenberg 1986; Holmes *et al.* 1989; Rappole 1995; Marra and Holmes 2001; Reitsma *et al.* 2002). In contrast, many species overwintering on the African continent move sequentially between various locations (Lövei 1989). This difference may arise because African migrants tend to be found in more open and seasonal habitats, and follow seasonal shifts in rainfall (Lövei 1989). Until data from a range of non-breeding Australo-Papuan migrants are available, it will remain unclear whether a particular dispersion pattern is most common here.

The key finding of our study is that at least some Buff-breasted Paradise Kingfishers are territorial at their non-breeding grounds. This is significant because it suggests competition for resources. Recent research has shown that competition (both intra- and interspecific) on the non-breeding grounds may be as, or even more, significant for limiting populations than processes operating during the breeding season (Greenberg 1986; Sherry and Holmes 1995). Such non-breeding-season competition has been inferred mainly from the existence of territoriality (Rappole 1995; Sherry and Holmes 1996).

Resource competition is also suggested when population densities differ among habitats, because it implies variation in habitat quality and thus competition for the better-quality habitats (Sherry and Holmes 1996). Although our data are too few to allow comparisons of density between habitat types, there was a hint from our study that habitat quality varied on a fine-scale for Buff-breasted Paradise Kingfishers. On all transects the territories clustered together, leaving some stretches that appeared to have no kingfishers present at all (Fig. 2). Moreover, in October 2000 one of us visited an area of structurally similar lowland rainforest on the floodplain of the Elevala River, a tributary of the Fly River in the Western Province of Papua New Guinea (~6°15′00″S, 141°30′00″E; 120 m above sea level). The response rate to playbacks was five times lower than for the Gahom study site (0.08 for 36 playbacks performed regularly over 2 km of small tracks), suggesting a lower density of birds.

The recent and well documented population declines of many North American–Neotropical migrants (e.g. Terborgh 1992; Martin and Finch 1995; Rappole 1995) is believed to be at least partly due to widespread habitat loss in the tropics, mediated by strong intra- and interspecific resource competition (Sherry and Holmes 1996). There is also good demographic evidence for population limitation during the non-breeding season for several European–African migrants that suffered population declines following drought years in sub-Saharan Africa (Baillie and Peach 1992). Many species of bird that breed in Australia migrate to New Guinea and south-east Asia. If it turns out to be generally true that competition at the non-breeding grounds is a major limiting factor for birds that migrate to (or within) these tropical regions, the looming broad-scale habitat loss in these areas (Sizer and Plouvier 2000) will cause declines in a large proportion of Australasian species. We urgently need more data on the non-breeding social systems, movement patterns and habitat preferences of species that migrate between Australia and New Guinea or south-east Asia.

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