Niche separation in African parrots

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Several taxa of African parrots are segregated by body mass and the three size classes (large parrot, small parrot and lovebird) differ markedly in Hutchinsonian ratios.

Greatest distributional overlap occurs between the large parrots (*Psittacus* and *Poicephalus* species) where niche separation equates with forest type and altitude, body mass, and feeding specialization. Several African parrot species of different body mass inhabit the same but specialized habitat type e.g. afromontane yellowwood forest (Cape Parrot and Yellow-faced Parrot) or semi-arid scrub (Rüppell's Parrot and the Rosy-faced Lovebird). All of the small *Poicephalus* parrots are allopatric although four species show partial distributional overlap with the similar-sized African Rose-ringed Parakeet. Coexistence between this parakeet and the four small *Poicephalus* species in their semi-arid environment may be mediated through low densities, different foraging behaviours (with respect to flight and bill morphology) and/or ecophysiology. Most lovebird (*Agapornis*) species are allopatric whereas the sympatric equatorial Red-faced Lovebird and Swindern's Lovebirds are separated by habitat and dietary preferences. Dietary specializations include feeding primarily on figs, grass seeds or the kernels of yellowwood fruits.

INTRODUCTION

The African psittaciform avifauna comprises about twenty species represented primarily by two genera, *Poicephalus*, the African parrots per se (10 species), and *Agapornis*, the lovebirds (7 species). The only other representatives are the African Grey Parrot, *Psittacus erithacus* and African Rose-ringed Parakeet *Psittacula krameri*. The African parrot guild has representatives in a wide range of habitats but is less diverse than those of South America, Australia and Indonesia (Forshaw 1989, Juniper & Parr 1998). This is attributed partly to the absence of very large species such as macaws (South America) and cockatoos (Australia), very small species such as the Budgerigah (*Melopsittacus undulatus*), and the absence of obligate nectarivorous species, such as the lories and lorikeets of Indonesia and northern Australia. Some of these niches in Africa are filled by three endemic families i.e. Musophagidae (turacos), Coliidae (mousebirds) and Lybiidae (African barbets), as well as by hornbills, trogons, sugarbirds and sunbirds (Maclean 1990). Africa has few associated islands, unlike Indonesia and the Pacific islands, and therefore no island species of parrots, unless the African Grey Parrot on Pincipé is different from the mainland form.

The aim of this comparative study was to investigate niche separation of African parrots with reference to their taxonomy, phylogeny, geographical distribution, body mass, habitat and diet.

Since allopatric species do not co-exist, they cannot compete and therefore they occupy different "geographical niches". If they have co-existed in the past, niche differences are attributed to the "ghost of competiton past". There might be niche convergences when species with allopatric distributions adapt to the same habitat or diet. Simberloff and Boecklen (1981) have argued for size segregation between congeneric species and Diamond (1986) has stipulated that such species should occupy equivalent guilds for this to be valid. These ideas and approaches are relevant to this study.

METHODS

Body measurements and body mass data were collected from specimens in the British Museum of Natural History at Tring and from birds handled during field studies (Wirminghaus *et al.* 2001, 2002, Symes & Perrin 2003, 2004, Taylor & Perrin 2006a,b, Selman *et al.* 2002, 2004, Warburton & Perrin 2005a,b, Ndithia & Perrin 2006). In addition to the field studies, distributional, altitudinal, habitat and dietary data were collected from the literature (Forshaw 1989, Juniper & Parr 1998).

RESULTS

Taxonomy

African Parrots comprise four genera, with a fifth, *Coracopsis*, occurring in Madagascar. The genus *Psittacus* is monotypic, but comprises the subspecies *timneh* as well as the nominate form *erithacus* (Forshaw 1989). In Africa, the only representative of the genus *Psittacula*, is *krameri krameri*, although many species occur in Asia and *P. echo* occurs on Mauritius (with several extinct species from the Indian Ocean Islands (Hume 2007)). The genus *Poicephalus* contains ten species (Table 1) if one accepts the Cape Parrot *P. robustus* as a separate species from the Brown-necked Parrot *P. fuscicollis* (Massa *et al*. 2000, Perrin 2005). The lovebirds are represented by seven species in Africa (Table 2)

with an eighth in Madagascar (*A. canus*), if one accepts that *A. personatus* is more than a melanic form of *A. fischeri* and that *A. nigrigenis* is more than a melanic form of *A. lilianae* (Racheli 1999, Eberhard 1998) (Table 2).

Body mass

African parrots fall very clearly into three body mass classes (Table 3), which is significant in niche partitioning. The large species (300–450 g) include the African Grey Parrot, the Cape Parrot, the Brown-necked Parrot (2 subspp.) and the smaller Jardine's Parrot (3 subspp.). All of the other *Poicephalus* species, and *P. krameri,* fall into the medium-sized class, while all of the *Agapornis* species are small. All African parrot species have a similar feeding mechanism (Homberger 1996) and belong to the same general trophic guild.

Distribution

Large parrots

The African Grey Parrot and Jardine's Parrot are sympatric in much of central Africa (Fig. 1) although not necessarily syntopic (see below). The Brown-necked Parrot (*P. f. fuscicollis*) exists as several small isolated (relic?) populations in West Africa while the allopatric Grey-headed Parrot (*P. f. suahelicus*) has a much wider distribution in central southern Africa (Fig. 2). Both of these forest species are separated from the central African populations of *Poicephalus* species by savanna woodland and grassland. The large parrot species cluster around the Congo Basin, extending to the north-west and south-east. The Cape Parrot is allopatric from each of these taxa and is confined to south-eastern Africa.

Small parrots

All of the seven species are alloptric or parapatric and none occur in association with the large parrot species in the tropical rain forests of West and Central Africa (Fig. 2). The common and widely distributed species of the northwest is the Senegal Parrot (*P. senegalensis*) and in Central Africa it is replaced by Meyer's Parrot (*P. meyeri*), which has the largest distribution of any African parrot. To the north-east, at higher altitude, occurs the Yellow-faced Parrot (*P. flavifrons*) and in the Horn of Africa the Red-bellied Parrot (*P. rufiventris*), whose distribution extends south to Kenya. Near the Kenya–Tanzania border, it is replaced by the Brown-headed Parrot (*P. cryptoxanthus*), with a coastal distribution extending to South Africa. Inland throughout its north–south distribution, it gives way to Meyer's Parrot, and ultimately, in the south-west, to the arid zone Rüppell's Parrot (*P. rueppelli*), which extends north through Namibia and Angola towards the equator. The distributions of these species seldom overlap, never extensively, nor in large numbers. The distribution of the Niam-Niam Parrot (*P. crassus*) in north-central Africa is parapatric and may overlap with that of the northern subspecies of Meyer's Parrot from which it most likely diverged (Massa *et al.* 2000). The only long-tailed parrot on mainland Africa, the Rose-ringed Parakeet, occurs in the Sahel, south of the Sahara, and overlap spatially in distribution with several of the small *Poicephalus* species.

Lovebirds

Apart from the nested sympatric distribution of Swindern's Lovebird (*A. swinderianus*) and the Red-faced Lovebird (*A. pullarius*), the remaining species are all allopatric (Fig. 3). The overall distribution of lovebirds matches in part that of the large parrots in that they are well represented in the tropical forest of the Congo basin and the small parrots in the arid zones of the north-east and south-west. A few species are widely distributed but most have small localized distributions, most of which are allo- or parapatric of each other. Swindern's Lovebird has a fragmented distribution with several populations in West Africa, although the main distribution is in equatorial Africa. In north-central Africa it is replaced by the Red-faced Lovebird. These two species have the largest ranges of any of the lovebirds. The little known Black-winged Lovebird has a confined distribution in the north-east while the Rosy-faced Lovebird inhabits the south-west of the continent. In East Africa, the Black-masked Lovebird and Fischer's Lovebird have small separate geographical ranges. This also applies to the two central-southern forms, the Black-cheeked Lovebird and Lilian's Lovebird.

Table 1. Phylogeny and mass categories of African parrots

Large Parrots		
	Genus *Psittacus*	*Psittacus erithacus* African Grey Parrot
	Genus *Poicephalus*	*Poicephalus robustus* Cape Parrot
		P. fuscicollis fuscicollis Brown-necked Parrot
		P. f. suahelicus Greyheaded parrot
		P. gulielmi gulielmi Jardine's Parrot
		P. g. massaicus
		P. g. fantiensis
Small Parrots		
	Northern clade	*P. rufiventris* Red-bellied Parrot
		P. flavifrons Yellow-faced Parrot
		P. senegalensis Senegal Parrot
	Southern clade	*P. meyeri* (six subspecies) Meyer's Parrot
		P. crassus Niam-Niam Parrot
		P. ruepelli Rüppell's Parrot
		P. cryptoxanthus Brown-headed Parrot

From Massa *et al.* 2000.

Table 2. Relationships of African lovebirds

Genus *Agapornis*		
	Northern, non-white eye-ring clade	
		A. swinderianus Swindern's Lovebird
		A. pullarius Red-faced Lovebird
		A. taranta Black-winged Lovebird
	Intermediate species	
		A. rosiecollis Rosy-faced lovebird
	Southern, white eye-ring clade	
		A. personatus Black-masked Lovebird
		A. fischeri Fischer's lovebird
		A. nigrigenis Blackcheeked Lovebird
		A. lilianae Lilian's Lovebird

From Racheli 1999.

Table 3. Average body masses (g) of African parrots

Group	Range	Average	Sample size
Large parrots	250–400	345	4
Small parrots	100–160	130	7
Lovebirds	30–60	40	8

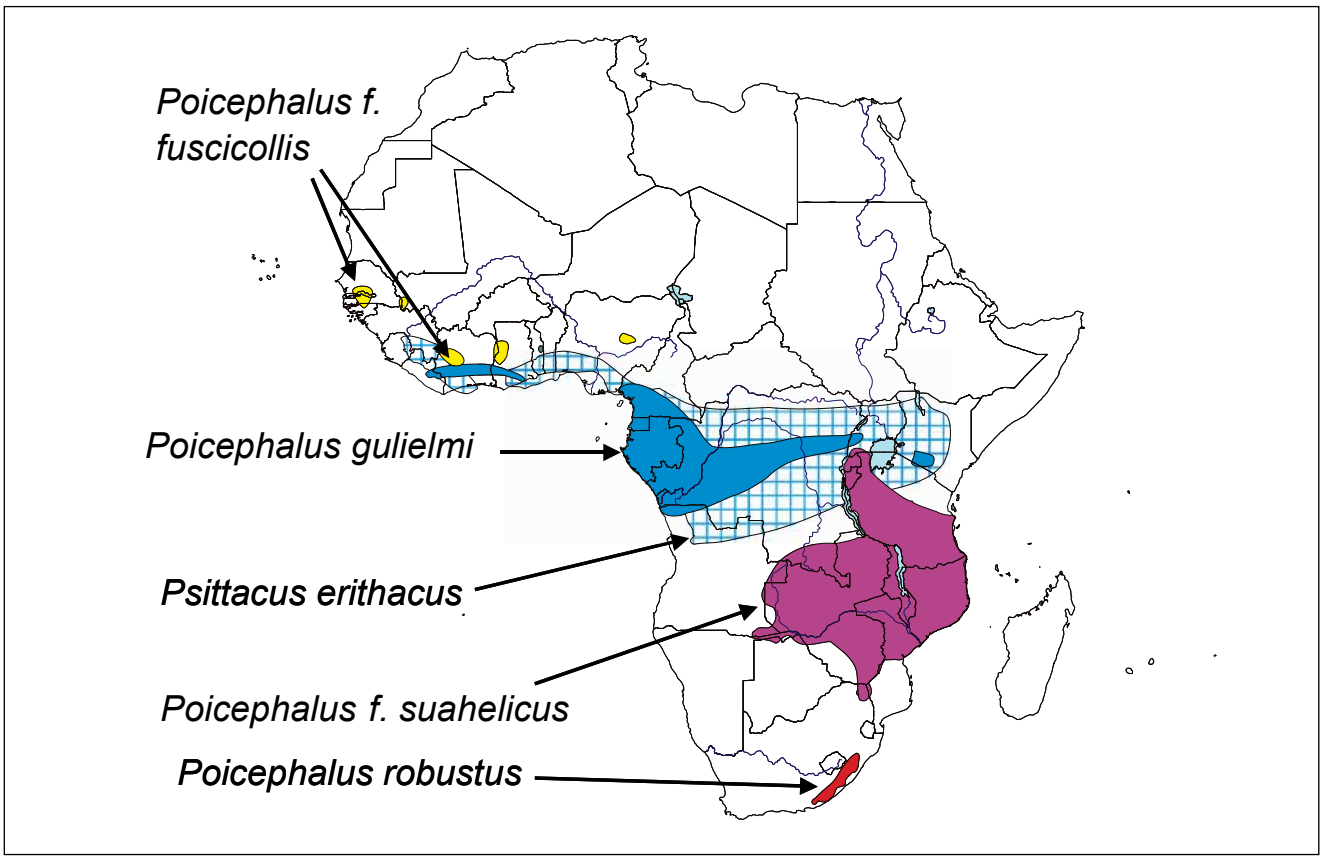

Fig. 1. Map showing the distribution of large African parrots.

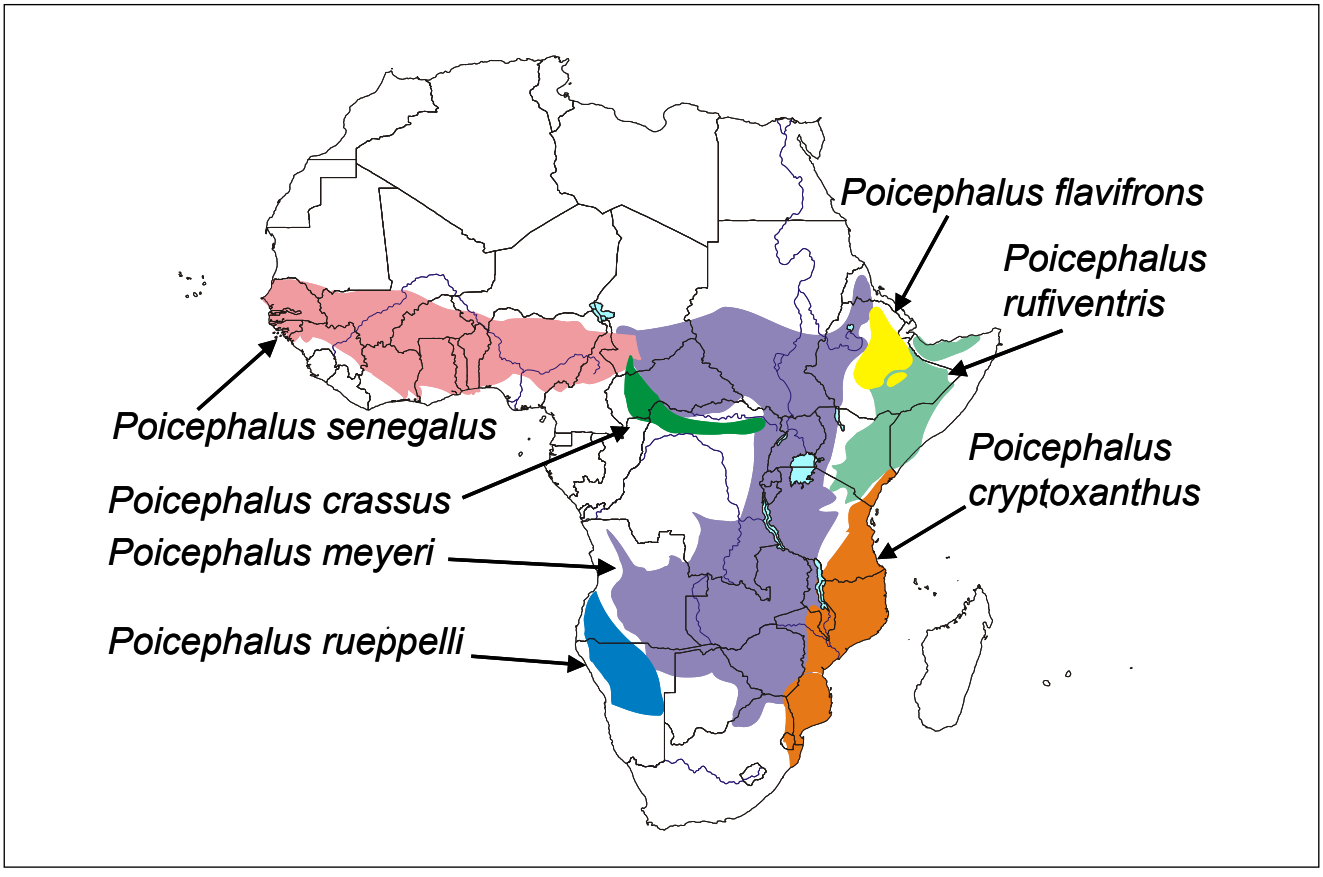

Fig. 2. Map showing the distribution of small African parrots.

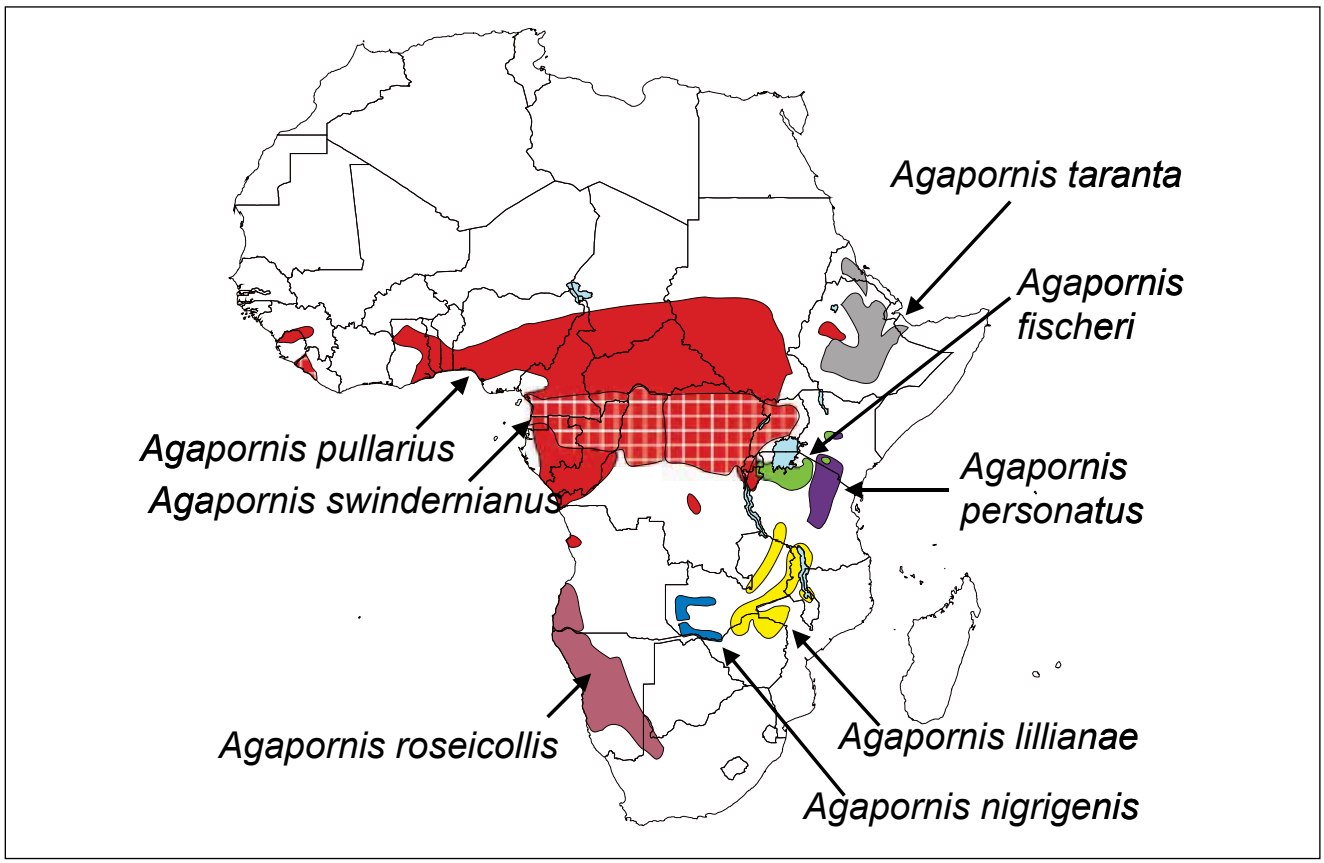

Fig. 3. Map showing the distribution of African lovebirds.

Habitat

Large parrots

Cape Parrots are habitat specialists in habiting afromontane yellowwood (*Podocarpus*) forest while Jardine's Parrot (subsp. *massaicus*) also occupies yellowwood and juniper afromontane forests (Table 4). Brown-necked Parrots and Grey-headed Parrots occur in a wide range of deciduous forest types, while the other two subspecies of Jardine's Parrot (*gulielmi* and *fantiensis*) both inhabit lowland forest types, where they are sympatric with the African Grey Parrot throughout most of its range.

Small parrots

The Yellow-faced Parrot (*P. flavifrons*) is an afromontane yellowwood forest specialist while Rüpell's Parrot (*P. ruepelli*) and the Red-bellied Parrot (*P. rufiventris*) are semi-arid species inhabiting dry grasslands and savannas (Table 5). The Brown-headed Parrot (*P. cryptoxanthus*) is a coastal forest specialist whereas the Senegal Parrot (*P. senegalensis*) prefers savanna grasslands/woodlands. Meyer's Parrot (*P. meyeri*, with six subspp.) is a habitat generalist occurring in habitats ranging from dry savanna to riparian woodland. The Niam-Niam Parrot (*P. crassus*), previously considered a subspecies on Meyer's Parrot, occupies wooded savanna in semi-arid environments. The Rose-ringed Parakeet is an adaptable habitat generalist like the Meyer's Parrot.

Lovebirds

The Black-winged Lovebird (*A. taranta*) only occurs in afromontane yellowwood-juniper forest while the other two none white eye-ring species, Swindern's Lovebird and the Red-faced Lovebird, inhabit lowland habitats, the former preferring forest and the latter lowland savanna (Table 6). The Rosy-faced Lovebird (*A. rosicollis*) is a habitat generalist in semi-arid environments. Fischer's Lovebird and the Black-masked Lovebird occupy lowland savanna and woodland while both Lilian's Lovebird and the Black-cheeked Lovebird are mopane (*Colophospermum mopane*) woodland specialists.

Table 4. Niche separation of large African parrots

Species	Mass (g)	Habitat	Diet
Cape	300–350	Afromontane forest	*Podocarpus* fruits
Grey-headed	300–400	Lowland woodland	Fruits and seeds (generalist)
Jardine's	250–300	Afromontane forest (*m*) Lowland forest (*f* & *g*)	*Podocarpus* & *Juniperus* fruits
African Grey	400–450	Lowland forest	Fruits and seeds (generalist)

Subspecies: *m* = *massaicus*, *f* = *fantiensis* and *g* = *gulielmi*

Table 5. Niche separation of small African parrots

Species	Mass (g)	Habitat	Diet
Yellow-faced	140+	Afromontane forest	Seeds & fruits (?)
Brown-headed	120–155	Coastal woodland	Fruits & seeds
Niam-Niam	120–150?	Savanna	Seeds (& fruits?)
Meyer's	100–135	Various woodlands	Catholic
Senegal	100–160	Wooded savanna	Fruits & seeds
Rüppell's	100–140	Semi-arid	Seeds & fruits
Red-bellied	~120	Semi-arid	Seeds & fruits

Table 6. Niche separation of African lovebirds

Species	Body mass (g)	Habitat	Diet
Swindern's	30–40	Evergreen forest	Figs, fruits
Red-faced	30–40	Lowland savanna	Grass seeds
Black-winged	50–60	Afromontane forest	Fruits, berries
Rosy-faced	45–60	Semi-arid	Seeds
Fischer's	42–58	Savanna woodland	Grass seeds
Black-masked	43–47	Lowland savanna	Grass seeds
Lilian's	30–35	Mopane woodland	Grass seeds
Black-cheeked	30–35	Mopane woodland	Grass seeds

Table 7. Diets of large African parrots

African Grey Parrot	Fruits and seeds of species of *Ficus, Alax, Heisteria, Dacryoides, Petersanthus, Combretum, Macaranga, Harungana, Ceiba, Lighia, Bombax, Celtis, Parkia* and *Prunus.*
Cape Parrot	Seeds of *Podcarpus* species predominantly. Occasionally fruits of *Olea, Mimusops*, *Calodendron* and *Commiphora* spp. (Wirminghaus *et al.* 2002).
Grey-headed Parrot	Fruits, seeds, nuts, berries and nectar of species of *Paranari, Ficus, Olea, Tterminalia, Calodendron, Harpophyllum, Mimusops, Acacia, Syzygium, Lannea, Diospyros* and *Zizyphus*. (Symes & Perrin 2003).
Brown-necked Parrot	No precise data available, likely similar to the Grey-headed Parrot.
Jardine's Parrot	Seeds and grains rather than fruits of *Olea, Spatheodea, Grevillea, Cedrus*, and *Podocarpus*. (Forshaw 1989).

Table 8. Diets of small African parrots

Meyer's Parrot	Seeds and grains rather than fruits of species of *Brachystegia, Combretum, Grewia, Sclerocarya, Ziziphus, Schotia, Ficus, Terminalia, Diospyros*, and *Garcina.* (Rowan 1983, Boyes & Perrin in press.)
Brown-headed Parrot	Fruits and seeds, or flowers, of species of *Adamsonia, Xanthocercis, Acacia, Albizia, Aloe, Erythrina, Strychnos, Cassia, Diospyros, Ficus, Kirkia, Lannea, Rhus, Sclerocarya, Terminalia* and *Trichillia.* (Taylor & Perrin 2006a).
Rüpell's Parrot	Fruits and seeds of species of *Terminalia, Tapinanthus, Acacia, Commiphora, Grewia Citrus, Combretum, Ziziphus, Ficus, Ximenia, Albizia, Boscia* and *Efretia*. (Selman *et al.* 2002).
Red-bellied Parrot	Fruits and seeds of species of *Ficus, Acacia, Balanites, Cordia* and *Dalbegia.* (Juniper & Parr 1998)
Senegal Parrot	Seeds, fruits and buds of species of *Kaya, Pterocarpus, Vitex, Parkia, Butyroaspermum, Adamsonia, Ximenia, Sclerocarya, Faidherbia, Cassia, Acacia,* and *Melina.* (Rowan 1983, Forshaw 1989, Juniper & Parr 1998).
Yellow-faced Parrot	Grain, seeds, fruits and occasionally leaves of species of *Adamsonia, Dovyalis, Bersama, Cordia, Diospyros, Ficus, Syzygium, Terminalia* and *Gymnosporia.* (Juniper & Parr 1998, Boussekey *et al.* 2002).
Niam-Niam Parrot	Poorly known: a variety of seeds, including millet, and grains. (Juniper & Parr 1998)

Diet

Most of the large African parrots feed on a wide range of fruits and seeds including some flowers, fruit pulp and insects, however, the Cape Parrot feeds predominantly on the kernels within the stone of yellowwood fruits while the Jardine's Parrot (subsp. *massaicus*) feeds largely on juniper berries and yellowwood fruits (Table 7).

The small parrots also feed on a range of fruits and seeds except for the Yellow-faced Parrot which is another juniper-yellowwood specialist (Table 8). The Rose-ringed Parakeet is a dietary generalist and opportunist.

Most lovebirds feed on seeds, particularly grass seeds, although the Black-winged Lovebird feeds largely on fruits and seeds of yellowwoods and junipers and Swindern's Lovebird is thought to specialize on feeding on figs (Table 9).

SYNTHESIS

Large parrots

Although sympatric, *P. g. massaicus* separates out on habitat, diet and altitude from its conspecifics. *Psittacus erithacus.* *P. g. gulielmi* and *P. g. fantiensis* separate out altitudinally and the former has a larger bill but a lower wing length to body length ratio, which may suggest differences in foraging and feeding behaviours (Table 10). *Psittacus erithacus* segregates from the former subspecies of *P. gulielmi* in having a much higher wing length to body length ratio, which may suggest foraging on dispersed foods, and from the latter in having a much larger bill, which may suggest feeding on larger fruits and seeds.

Small parrots

The small *Poicephalus* species separate out precisely in their distribution. The Yellow-faced Parrot is a habitat and dietary specialist while Meyer's Parrot is a habitat and dietary generalist. Most other species are dietary generalists, however, the Red-bellied and Rüppell's Parrots are semi-arid zone species, Senegal and Niam-Niam Parrots occur in woodland savanna, and the Brown-headed Parrot is restricted to coastal forest.

The Rose-ringed Parakeet is sympatric along a longitudinal gradient with Senegal, Meyer's, the Yellow-faced and the Red-bellied Parrots from west to east. Its body mass is only slightly larger than these other species, thereby likely

Table 9. Diets of African lovebirds

Red-faced Lovebird	Principally seeds of tall grasses, often eaten green. Occasionally fruits. (Chapin 1939)
Black-winged Lovebird	Tree fruits including figs and berries of *Juniperus*, but also seeds.
Swindern's Lovebird	Fruits of Strangler Figs *Ficus* spp., accasionnaly seeds. Flowers of *Spathedea*. (Chapin 1939, Friedman & Williams 1969)
Rosy-faced Lovebird	*Anthephora schinzii* is preferred although many species are eaten. Grass seeds of *Pennisetum mezianum*, seeds of erect herbaceous plants e.g. *Achyranthes* spp., occasionally seeds of *Albizia* and *Acacia (karoo* especially), fruits of *Ziziphus mucronata*, *Rhus villosa* and *Commiphora* spp., and *Ficus* spp. (Ndithia & Perrin 2006a)
Fischer's Lovebird	Mainly grass seeds, especially *Pennisetum mezianum*. Also seeds of *Acacias*, fallen berries of *Ligustrum lucidum*, fruits of *Ficus* figs, *Rhus villosus* and *Commiphora* spp. (Forshaw 1989, Juniper & Parr 1998)
Black-masked Lovebird	Diet consists of the seeds of grasses.
Lilian's Lovebird	Grass seeds predominantly e.g. *Hyparrhenia* spp., seeds of annual herbs and *Acacia* spp., flowers of several tree spp., e.g. *Faidherbia* and *Erythrospermum* spp. (Rowan 1983)
Black-cheeked Lovebird	Annual grass seeds predominantly e.g. *Echinochloa, Chloris* spp., also seeds of annual herbs, and of trees e.g. *Albizia, Rhus* and *Combretumn* spp. (Warburton & Perrin 2005a)

Table 10. Fine niche resolution of large African parrots

Species	*P. erithacus*	*P. g. gulielmi*	*P. g. fantiensis*	*P. g. massaicus*
Altitude (m asl)	<2000	400–1000	<400	1800–3700
Rainfall (mm)	1000–2000	2000–3000	2000–3000	1000–2000
Bill (mm)	34.5±1.4	34.1±1.7	29.7±1.7	29.1±1.8
Wing–body (ratio)	80.5	69.3	76.5	77.0

negating size segregation, and the parakeet is a habitat and dietary generalist. One therefore wonders if there is niche overlap and competition between these species. The mostly likely case would be between the Rose-ringed Parakeet and Meyer's Parrot, as both have wide distributions, inhabit several habitat types and feed on a wide range of foods. Relative population densities in the semi-arid environments where they co-occur, and where productivity is low, might minimize competition. Differences in tail and wing dimensions may affect their foraging behaviour while differences in bill dimensions likely influence food preferences, but this is speculative. Alternatively, the two species may be competing for food and nest sites.

Lovebirds

The congeneric (or conspecific) lovebird pairs, Fischer's and Black-masked, and, Lilian's and Black-cheeked, are allopatric within and between these pairs, so each is geographically separated. The former pair inhabit lowland wooded savanna while the latter pair inhabit mopane woodland. All are predominantly graminivorous. The Rosy-faced Lovebird is a semi-arid allopatric species that feeds on a variety of seeds, and which, taxonomically, is likely intermediate between the white eye-ring and the non-white eye-ring species.

The Black-winged Lovebird is a habitat and dietary specialist, feeding on fruits and berries in afromontane forest. Swindern's and the Red-faced Lovebird are sympatric and both occur in similar habitat types, however, the former feeds on fruits, particularly figs, while the latter feeds on grass seeds. This suggests that the two species may not be syntopic. (The Grey-headed Lovebird of Madagascar is a lowland habitat generalist that feeds largely on grass seeds).

DISCUSSION

Large parrots

Most species of African parrots inhabit forest-woodland habitats while fewer species inhabit mopane woodland, grassland savanna and semi-arid scrubland vegetation types. It can be inferred that the ancestral *Poicephalus* parrot was a forest species, with later taxa colonizing woodland, savanna, and semi-arid scrub.

The *Poicephalus* parrot species comprise the large Cape Parrot, the closely-related subspecies pair of the Brown-necked Parrot and the Grey-headed Parrot, and Jardine's Parrot, of which there are three distinct subspecies. The Cape Parrot has a southerly distribution comprising two major sub-populations in the E Cape and KwaZulu-Natal of South Africa. A few birds may remain in the north of the country near the Soutspanberg mountain range. They are distinct from the parapatric Grey-headed Parrot in having distinct habitat requirements (Symes 2001, Symes *et al.* 2000, Symes & Perrin 2003c, in press). If they are not geographically separated they are certainly ecologically separated. The former occurs in afromontane yellowwood forest and the latter in various woodland habitats, ranging from mopane woodland and mixed broadleaf woodland to secondary growth forest. Grey-headed Parrots are geographically separated from Brown-necked Parrots, which occur in the Congo basin of West Africa. They are geographically distinct, but these two forms are more closely related to each other than either is to the Cape Parrot, and their habitat preferences and ecologies are not dissimilar.

Within the Jardine group, *P. g. gulielmi*, has by far the widest and largest distribution in central Africa, but with a

discontinuity. The considerably smaller *P. g. fantiensis*, has the most westerly distribution in West Africa but also occurs as two separate subpopulations, whereas *P. g. massaicus* occurs in the east as a single distinct subpopulation. It inhabits yellowwood and juniper forests in Kenya and Tanzania (while in Ethiopia this habitat niche is filled by the Yellow-faced Parrot). *Poicephalus g. gulielmi* occurs at 400–1000 m asl while *P. g. fantiensis* occurs below 400 m asl, so the subspecies pair is altitudinally segregated.

The African Grey Parrot and the latter two subspecies of *P. gulielmi* occupy lowland forest but are segregated by habitat and geographically: there are also differences in morphology. For example, *P. g. fantiensis* has a smaller bill than the African Grey Parrot (29.7±1.7 versus 34.5±1.4) while *P. g. gulielmi* has a lower wing length to body length ratio than the African Grey Parrot (69.3 versus 80.5), which may influence their foraging behaviours.

The African grey Parrot is widely distributed in Central and West Africa where its range overlaps with that of several other parrot species. Sympatry (or parapatry) with the Senegal Parrot in the west and Meyer's Parrot in Central Africa is not surprising owing to the marked difference in size and hence food and other (e.g. nest site) resources. The habitat of the Senegal Parrot is also different from that of the African Grey Parrot.

The Brown-necked Parrot, although co-occurring with the African Grey Parrot in West Africa, generally occurs further north and inhabits savanna rather than forest, gallery and riverine woodland. In the east, where the Brown-necked Parrot is replaced by the Grey-headed Parrot, habitat segregation persists, with the African Grey Parrot occurring in the forests and the Grey-headed Parrot in savanna woodland.

Small parrots

The Meyer's Parrot subspecies group comprises two distinct clusters, *senegalus* with *rufiventris*, and *meyeri* with *cryptoxanthus*. The former "red or yellow billed species" pair, although genetically similar, and inhabiting the dry sahelian region, are very widely separated geographically. The Senegal Parrot is widely distributed throughout West Africa, north of the equatorial forests, whereas the Red-bellied Parrot has a more restricted, although nevertheless, wide distribution, from Tanzania north through much of the Horn of Africa. Both species prefer semi-arid woodland-savanna, are similar-sized and have similar diets, so niche separation is geographical. The Senegal Parrot occurs as three subspecies (*senegalus, versteri* and *mesotypus*) whose modes of niche differentiation have not been recorded. The other species form the "green" forms, which inhabit riverine forest and a range of woodland habitats, consisting of the Brown-headed Parrot inland form, distributed much along the eastern seaboard from South Africa to southern Kenya, and the very widely distributed Meyer's Parrot which occurs through much of the African interior but not on the eastern seaboard. Ecological separation is geographical for the smaller African parrots although there is some habitat separation; they exploit similar foods. The Yellow-faced Parrot inhabits afromontane, juniper-yellowwood forest, Brown-headed and Niam-Niam Parrots woodland or woodland savanna, Senegal and Meyer's Parrots savanna and Rüppell's Parrots and Red-bellied Parrots semi-arid grasslands.

The Niam-Niam Parrot is closely related to Meyer's Parrot and has a sympatric or parapatric distribution in Chad and the Central African Republic. There are no clear ecological differences between the species pair which is suggestive of competition. Therefore, there might be strong selection pressure operating to cause niche divergence between them. It can only be assumed that there are significant differences in courtship, perhaps including vocalizations, maintaining the separate gene pools.

Rüppell's Parrot is a derived, arid zone species, occurring in south-western Africa, largely allopatric, except in the east of its range where it co-occurs with the generalist Meyer's Parrot. Niche separation is by habitat, the former inhabiting xeric woodland or savanna and the latter forest or riverine woodland. The Yellow-faced Parrot is another narrow niche species found in the highland yellowwood and juniper forests of Ethiopia where it co-occurs with the Red-bellied Parrot, which occupies semi-arid bush vegetation. Habitat may result in different foods and segregate the niches of the species pair.

Lovebirds

Most lovebirds are grassland or savanna species, but the white eye-ring (social and dimorphic) species are thought to have been derived from the non white eye-ring (solitary and monomorphic) species, which are predominantly forest or woodland species. A similar colonisation and radiation may have occurred as inferred for the small parrots.

The non-white eye-ring species have a more northwestern distribution in sub-Saharan Africa whereas the white eye-ring species are more south-easterly in their distribution. The latter taxa (or clade, white eye-ring species) are thought to be derived from the former, and the genus *Agapornis* is likely derived from the hanging parrot genus *Loriculus* of Asia (Forshaw 1989, Eberhard 1998). This suggests that the Grey-headed Lovebird likely colonized Madagascar from Africa before the separation of the white eye-ring species in Africa.

Coexisting Swindern's Lovebird and the Redfaced Lovebird

Swindern's Lovebird is an arboreal species wholly dependent on evergreen, often gallery forest. It feeds on figs and insects and may be dependent on or has co-evolved with *Ficus* figs that fruit year-around. It is an obligate fig-eater. Bordering the forests inhabited this species are woodlands and grasslands occupied by the Red-faced Lovebird, which is graminivorous, a grass seed eater. It is dependent on holes or excavations in the nests of arboreal ants and termites for its nesting sites.

South-west of Lake Victoria, Red-faced Lovebirds are lowland tropical birds, while the former only occurs below 600 m asl. *A.p.guineensis* occurs below 700 m asl while its conspecific *A.p. pullarius* is distributed between 400 and 1200 m asl. The southern limit of its distribution is a barrier of high ground west of lakes Albert, Edward and Kivu. South-west of Lake Victoria, The Red-faced Lovebird and Fischer's Lovebird are parapatric and the breeding ranges may overlap slightly, but they are isolated reproductively by the specialized nesting habits of the Red-faced Lovebird.

The Black-winged Lovebird: an altitudinal specialist

The Black-winged Lovebird is a highland specialist inhabiting juniper and euphorbia thickets at altitudes of 1650–2470 m asl. In the eastern limits of its distribution, the Red-faced Lovebird occupies the lower slopes of the upland plateau inhabited by the Black-winged Lovebird.

Table 11. Species diversity of African parrots: number of species per habitat

Species	Afromontane forest	Lowland forest	Wooded savanna	Mopane woodland	Grassland savanna	Semi-arid scrub
Large	2	3	0	0	0	0
Small	1	2	4	0	2	2
Lovebirds	1	1	2	2	1	2
Total	4	6	6	2	3	4

The remaining five species inhabit deciduous woodland and bush that experience a severe long dry season.

Fischer's and Black-masked Lovebirds: closely related, allopatric generalists

Fischer's Lovebird and the Black-masked Lovebird dwell on the interior plateau of Tanzania between 1000–1500 m asl. The distribution of Fischer's Lovebird is bounded in the east by the forested mountains of the Rift Valley wall, and in the north, by Lake Victoria; but its southern and western limits have no obvious geographical barrier. The range of the Black-masked Lovebird is bounded in the east by the low land of the Pangani Valley and in the south by the forested mountains of Nguru, Ukaguru, Usagara and the Iringa Highlands, usually 1650 m asl. In the northern half of its range, the Black-masked Lovebird approaches within 60 km of that of Fischer's Lovebird, but nowhere are they contiguous. Neither of this species pair is highly specialized, and both inhabit grassland with scattered trees and shrubs, breed commonly in Baobabs in the same season and use a very similar variety of nesting sites. They feed on grass and Acacia seeds although details of the diet in the wild have not been quantified. Each species may form loose flocks of up to 100 birds and move locally in relation to food availability. The ranges of both species may be limited by miombo (*Brachystegia-Isoberlinia*) woodland, but why this should be so is unclear. There are few heavily seeded grasses and the seeds of the dominant leguminous trees are wide and flat, rather than small and spherical, unlike those in the preferred part of their range. Whatever the cause, miombo woodland is shunned by both of these lovebirds.

Black-cheeked Lovebird and Lilian's Lovebird: closely related, allopatric species pairs

Both of the southern forms, the Black-cheeked Lovebird and Lilian's Lovebird, are low altitude species occurring at 400–1000 m asl and 600–1000 m asl respectively. The Black-cheeked Lovebird has a very localized distribution in the river valleys of mopane woodland. It is a predominantly graminivorous but also feeds on leaves and flowers. Lilian's Lovebird has a wider range but it is also confined to mopane woodland in lowland hot, river valleys where it feeds on grass seeds and in Acacia species. In the north its distribution is bounded by miombo woodland. The distributional ranges of the two species are separated by 80 km but they are nowhere contiguous. Any valid reason for niche separation is difficult. Recently, it has been shown that the availability of standing water limits the distribution of the Black-cheeked Lovebird (Dodman 1995a,b, Warburton 2003).

The Rosyfaced Lovebird: a loner

The Rosy-faced lovebird ranges from sea level to 1370 m asl in semi-arid environments, and is a generalist feeder. It is geographically widely separated from other species.

To summarise, the spatial characteristics of the lovebirds are as follows (Moreau 1948): Swindern's Lovebird and the Red-faced Lovebird are in part parapatric but their diets are different; The Red-faced Lovebird is isolated by altitude: the Red-faced Lovebird overlaps slightly with Fischer's Lovebird but has specialized nesting requirements; Fischer's Lovebird and the Black-masked Lovebirds are allopatric but their ranges are close to one another and ecologically they are very similar; the Black-cheeked Lovebird and Lilian's Lovebird are allopatric but they are very similar.

All species, parrots and lovebirds

The highest species richness of all psittacine species occurs in lowland forest and woodland, and comprise all size classes, although, several species, of all size classes, inhabit afromontane yellowwood (-juniper) forest (Table 11). Mopane woodland has been colonized by two taxa of lovebirds, and semi-arid scrub by four taxa of psittacines. The size separation of African partrots is mirrored by the Madagascan parrot species, that is the large Vasa Parrot *Coracopsis vasa* , the smaller Black Parrot *C. nigra* and the Grey-headed or Madagascan Lovebird *A. canus*.

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