

Ethology and Ecology of the Patas Monkey (*Erythrocebus patas*) at Mt. Assirik, Senegal

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Abstract: We report ecological and ethological data collected opportunistically and intermittently on unhabituated patas monkeys at Mt. Assirik, Senegal, over 44 months. Although unsystematic and preliminary, these data represent the most ever presented on far western populations of the West African subspecies (*Erythrocebus patas patas*). Patas monkeys at Assirik live in a largely natural mosaic ecosystem of grassland, open woodland and gallery (riverine) forest with a full range of mammalian predators and competitors but without domestic plants and animals. All sociological variables measured fall within the range of patas monkeys studied elsewhere in East and Central Africa, but apparent nuanced variation could not be tested, given the lack of close-range, focal-sampled data. This awaits further study.

Résumé: Des données écologiques et comportementales ont été récoltées de façon opportuniste et discontinue durant 44 mois sur les patas sauvages à Mont Assirik, Sénégal. Malgré leur nature préliminaire et non-systématique, ces données sont actuellement les plus nombreuses sur la sous-espèce d'Afrique occidentale (*Erythrocebus patas patas*). Les patas de Mont Assirik vivent au sein d'un écosystème constitué d'une mosaïque de savanes herbeuses et boisées avec des forêts galeries, en présence de nombreuses espèces de mammifères prédateurs et compétiteurs, mais en l'absence de toute plante ou animal domestique. Nos résultats montrent que les patas de Mont Assirik ressemblent à ceux d'Afrique de l'est et d'Afrique centrale de façon générale, mais des analyses approfondies des variables socio-écologiques requièrent des données systématiques sur des individus habitués à la présence des observateurs.

Key words: Patas monkey, *Erythrocebus patas*, behaviour, habitat, West African primates

INTRODUCTION

The main aims of the study were to: (a) compare the main features of the socioecology of patas monkeys (*Erythrocebus patas*) in Senegal to those noted elsewhere in Africa, and (b) investigate the general ecology of patas in a mosaic of mixed woodland and grassland in far western Africa.

Most recent studies have been done in East Africa on *E. p. pyrrhonotus* or in Central Africa on *E. p. patas*. Both of these long-term studies, at Laikipia in Kenya (Chism & Rowell 1986, 1988; Enstam & Isbell 2002, 2004; Isbell & Chism 2007; Pruetz

2009; Burnham & Riordan 2012) and Kala Maloue in Cameroon (Ohsawa *et al.* 1993; Nakagawa 1999, 2000, 2003; Ohsawa 2003), have lasted for decades and systematically have compared patas with sympatric guenons. We report data on the largely neglected, far West African sub-species of patas monkey (*E. p. patas*), found from Senegal to Chad (Isbell 2013).

The first systematic study of patas was done on grassland savannas in Uganda, toward the eastern end of the species' range (Hall 1965). Struhsaker

and Gartlan (1970), Gartlan and Gartlan (1973) and Gartlan (1975) later studied a central African population of patas in the more arid Sahelian savannas of Cameroon. All of their observations seem to have been done at waterholes in the dry season. The species' range extends westward from Cameroon for another 3000 km, to the Atlantic Ocean. In pelage, western populations are subspecifically different, lacking the contrasting pattern of facial hair, but they are similar in morphology and dimensions to the eastern forms (Isbell 2013).

The only previous reports on the socioecology of far western patas are brief or lack detail. Galat-Luong *et al.* (1994, 1996) studied patas in coastal Senegal, in the Saloum Delta National Park, on the northwestern side of the country. Chism and Rowell (1988) studied patas for 4 weeks at Tenzugu in Ghana, a depauperate, highly human-modified site where the patas raided crops daily. Pruetz and Marshack (2009) reported chimpanzees (*Pan troglodytes verus*) preying on patas in southeastern Senegal, at Fongoli.

STUDY AREA AND METHODS

From February 1976 to December 1979, the Stirling African Primate Project (SAPP) maintained a small field camp (12° 53' N, 12° 46' W) by one of the main watercourses draining from Mont Assirik (elevation: 311 m). Two to four observers at a time concentrated on studying the chimpanzee, and in 1977, fulltime studies began on both Guinea baboons, *Papio papio* (Sharman 1981) and green monkeys, *Chlorocebus sabaeus* (previously *Cercopithecus aethiops*; Harrison 1983a, 1983b).

Vegetation

McGrew *et al.* (1981) presented quantitative data on climate and vegetation at Assirik. The slopes of the low, flat-topped hill are covered in deciduous woodland and bamboo (*Oxytenanthra* sp.) and merge into basins dominated by tall elephant grass (*Andropogon* sp.) with occasional, isolated trees. These basins are separated by a series of flat laterite plateaux ('bowes'), covered mainly by *Danthiopsis* sp. grass. Some areas of plateaux have scattered *Combretum* bushes, *Acacia* scrub, or coarser vegetation in poorly-drained places. Seasonal streams cut through the plateaux in rocky gorges and provide the only suitable sites for the small strips of gallery forest with evergreen trees. Other

ridges and slopes support further deciduous open woodland. Thus, four distinct habitats – forest, woodland, plateau, and grassland – cover most of the study area. Within the study area, only one stream has permanently flowing water. By the end of the dry season (March-May), the only other surface water comprises small pools in streambeds at about eight sites in steep-sided valleys.

Fauna

Five potential mammalian predators on patas occurred at Assirik: lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), African wild dog (*Lycaon pictus*), and side-striped jackal (*Canis adustus*). All were encountered occasionally year-round, although most were nocturnal (McGrew *et al.* 2014). Large predatory reptiles such as Nile monitor lizard (*Varanus niloticus*) and Nile crocodile (*Crocodylus niloticus*) also occurred in the study area (McGrew 2014).

Assirik had no domesticated animals or plants, thus no crop-raiding nor provisioning. There was little sign of anthropogenic modification of the habitat, apart from the annual burning mentioned above: no water tanks, fence lines, charcoal-making, or forest clearance. The fauna and flora in 1976-79 was typical of the Guinea-Soudanian woodland of the Sahel, including the presence of elephants (*Loxodonta africana*). Some small-scale illegal hunting occurred, but there was no evidence of human killing of patas.

Climate and Seasonality

Four years (1976-79) of records of temperature, rainfall, relative humidity, and cloud cover show that Assirik undergoes a pronounced dry season with highest temperatures towards its end in April and May (McGrew *et al.* 1981). Annual rainfall varied from 824 -1224 mm (median = 885 mm), with much rain from June to October and almost no rain between November and May. By mid-November, grasses were dead and highly inflammable; bushfires swept through plateaux and basin grasslands. Only the gallery forest escaped severe fires and even there leaf litter often burned. The blackened, leafless and arid appearance of most of the Assirik region during the dry season belies the fact that many trees and shrubs then come into flower, such as *Pterocarpus erinaceus*, *Bombax costatum* and *Combretum* sp., whilst others (e.g., *Adansonia digitata*) produce ripe fruits at this season.

Data Collection

All SAPP researchers occasionally encountered patas and took notes on group size, habitat, and general behaviour. As these observers concentrated on the other three species of diurnal primates, they spent most of their time in gallery forest or woodland and rarely saw patas in these biomes. Encounters usually happened as researchers crossed plateaux en route to other areas or when taking the hourly meteorological readings on the plateau at camp.

Most of the observations beyond brief glimpses were of monkeys as they drank, rested, moved, or foraged across extensive open spaces. The terrestrial observer usually was several hundred metres distant, so even thin vegetation cover was a visual hindrance. During the middle of the day, heat shimmer greatly reduced the effectiveness of binoculars. It was rarely possible to record continuous sequences of behaviour, to make regular time samples of activity, or to ascertain the exact composition of a group by age and sex. Here, we based analyses on putative breeding groups in which infants were seen, or on an adult male with females, or on groups larger than six, i.e., greater than the largest all-male group ever seen at Assirik.

We opportunistically collected patas faecal samples and examined them by sluicing and sieving (McGrew *et al.* 2009).

From late November 1977 to late January 1978, observations were made sitting quietly, monitoring a waterhole near camp that was visited by patas for drinking.

From 1978, we used notecards with standardised categories of data for patas. At each encounter, observers recorded initial and final distance to encountered monkeys, how monkeys reacted, and details of their departure. Observation distances varied with season, location, and with circumstances (see below). Thus, 126 encounters were classed by:

- (a) type of response: i.e., fleeing; undisturbed activity (such as feeding, or continued relaxed presence, for more than 3 min.); or ambiguous response (much vigilance or unhurried movement away)
- (b) season: July-November (wet, poor visibility) or December-June (dry, after burning, so improved visibility);
- (c) locality: Home (plateau around camp constantly crossed by SAPP researchers) or Away (other places);
- (d) Observer circumstances: on foot or from vehicle.

CH spent 5 November – 2 December, 1979, at Assirik. He employed a mixed strategy of extensive survey walks and long-range scanning with binoculars of plateaux. He made spot-checks from a vehicle at places where patas had been seen before and that were visible from the 2.8 km of motorable track. Besides intensive observations in the same areas close to camp, CH twice visited eight of the nine major outlying plateaux within the usual SAPP survey region.

RESULTS

Social Interaction

Patas showed remarkably little physical or vocal interaction that could be detected by observers from a distance of 50 m or more. Monkeys sat near or moved past others in a relaxed way, with no obvious display signals or signs of avoidance. Those resting in the same tree were often several metres apart. In 17 encounters totalling 481 min of relatively undisturbed observations, mainly around a waterhole, social grooming occurred only three times.

We saw 15 instances of chasing play. Nine times, juveniles or infants usually took part, but once an entire large group romped around together. Another time, two pairs of adult females chased and play-grappled for ca. 6 min before following the rest of the departing group.

We saw no adult sexual behaviour, but once a juvenile entered a group and briefly mounted another, clasping with the hands on the back. There was a marked birth season: two heavily pregnant females were recorded in February, whilst young infants, which are dark in colour and carried ventrally, were recorded between February and May, with a peak in March. After early June, all infants had the coat colour of fully-grown females and rarely were carried, except during disturbances.

Group Dispersion

Patas groups often spread over a wide area, so that recording of group scatter was possible only in fairly open situations. The range of dispersion distances ($n = 35$) were from 15-300 m, with most records at 30-150 m. Larger groups (10 or more members) had a median dispersion of 125 m, almost twice that of smaller groups at 60 m.

Progression Order

We made only nine fairly comprehensive identifications of individuals in progression orders; in 18 other cases, we had data only about the easily identified adult male. We analysed the data for individual position in the group for each age-sex class in terms of first in progression, last in progression, leading and trailing four individuals, and individuals in the middle between the first and last four. Juveniles and infants never were first in a moving group. Adult males were never in the middle but instead were either in the leading section or, often, at the rear. Adult females occurred anywhere in the progression order.

Several times an adult male moved through a static group from one side to the other, and males often showed vigilance at the edge of a group. But the adult male of a group was sometimes far from it: several times a group of females was watched for many minutes before a male appeared, or vice versa. Once, an adult male appeared out of woodland, 250 m away from a group of 10 females and young, whom he joined/rejoined.

Relations with Other Species

Patas regularly were seen close to ungulates, taking little notice of oribi (*Ourebia ourebi*) or bushbuck (*Tragelaphus scriptus*). They avoided the larger roan (*Hippotragus equinus*) and hartebeest (*Alcelaphus buselaphus*) if these bovids approached too closely. Once a group of 14 patas, including three young infants, fled from the observer to a line of *Combretum* bushes where there were already two jackals. There was no sign of tension between the two species, although the monkeys were as close to the jackals as 5 m on the ground and 2 m in the vegetation, before the group moved off foraging. A group of patas called continuously, with a lion resting in tall grass 100 m away; they continued calling (but type of vocalisation was unspecified) for 30 min from the same place before moving back into woodland.

Patas behaved differently toward green monkeys versus baboons. Several times green monkeys were seen close to patas on the ground or feeding in a tree within 1 m, with no sign of interaction. In contrast, patas avoided baboons as soon as they were seen or heard, except for one occasion toward the end of the dry season. Then the patas came down to a waterhole only 40 m from a noisy baboon troop and approached as close as 5 m to one juvenile baboon.

Patas treated observers the same way they treated baboons.

Full analysis of the data on encounters with observers was handicapped by observations being distributed unequally. For example, there were only 15 observations from vehicles, and, excluding these, other combinations of variables (see above) ranged from 4–19 cases.

Using only Away data and keeping seasons separate, the median response distances (from observer to nearest patas) were: for Fleeing, 80 m in dry season and 70 m in wet season; for Undisturbed, 300 and 170 m; for Ambiguous response, 200 and 175 m.

For vehicular observations, using the Away data for Undisturbed and Ambiguous responses combined gave a median distance of closest observation of 50 m, whilst on foot the median was 200 m. At the Camp waterhole, patas often showed undisturbed behaviour at about 70 m. Thus, a quiet, immobile observer on the ground seemed to be equivalent to one watching from a vehicle, but this may have been confounded by a context-specific habituation effect (see below).

Detection of genuine habituation of patas to observers close to camp was difficult. For outright Fleeing, median distances of encounters were identical (75 m) for Home versus Away. For Undisturbed and Ambiguous encounters, mode of observation was equated by eliminating from the Home records cases in which the observer was sitting quietly outside the hut that overlooked the waterhole. For the remaining data, the median observation distances for Home versus Away were 165 versus 200 m for Undisturbed responses and 80 versus 200 m for Ambiguous responses. Thus, Home observation distances tended to be shorter than Away. Some groups that often were active around camp seemed to become partly habituated to human activity. Once, when two groups of patas interacted, the observer moved to within 20 m of them without their showing any obvious response, although this may have been because they were preoccupied with each other.

The monkeys' main escape response to an observer was to move away on the ground. During four Fleeings and 45 Ambiguous responses, patas only once climbed trees and even that was transient. If they were encountered first in trees, then the monkeys climbed down immediately or moved across to the next tree before descending. However, patas that moved away from an observer often disappeared into scrub or woodland cover or paused

and climbed up into *Combretum* bushes. Movement into cover occurred in 25 cases of fleeing versus seven cases of climbing into vegetation. This difference was not due to just environmental necessity, as movement into cover was noted only four times in both Ambiguous and Undisturbed conditions. Some climbing was noted in about half of feeding bouts and in four Ambiguous withdrawals. Thus, when cover from bushes or trees was nearby, patas actively used it in escape from some disturbances.

Although males were often the last of a group to leave, threats or distraction (branch-shaking, hindquarter bouncing, yawning toward observer) were unusual. Even when undisturbed, patas spent much time scanning their surroundings, often from bushes, rocks or termite mounds.

Vocalisations

In most encounters with humans, patas made no audible calls, although only rarely were observers closer than 50 m. Thus, the monkeys may have used low-intensity calls that were undetected by observers. We noted four distinct types of call:

Repeated barking by adult males and 'chirrup' calls by breeding groups were as reported by Hall (1965) but we also heard two other vocalisations:

Squeal: "peeyow". The context of this call was unclear, but it was heard most often when a large group of patas hesitantly approached a waterhole in the gallery forest, with baboons close by. Once, a barely independent infant squealed when bitten by an adult female. Calls recorded as "cat-like miaouw", "mew", or "thin wailing" may have been variations of Squeal.

Growl: "(g)rrr" sound audible at about 40 m.

Growls were heard from a large group as they crossed a wooded ravine, and from another group in the presence of what was probably a strange adult male. In the latter case, growling also was the second component of a double call with the bark and was probably given by the solitary adult male.

Thus, calls audible at 40 m or more distance were prompted by some disturbance from outside the group, either by observer, potential predator, or extra-group patas.

Eating and Drinking

Feeding was recorded whenever a monkey put its hand to the substrate and then immediately up to

its mouth. Sometimes items were seen to be picked up and eaten, but at long-range, and sometimes even at close range, small items such as insects or seeds were unidentifiable. Monkeys turned over stones in order to inspect exposed cavities and swept the hand through ground litter.

Pooling feeding incidents by hour of the day suggests that peaks of activity occurred in mid-morning and late afternoon. Changes in observer activity were accounted for by calculating the hourly rates of feeding per 10 encounters with patas. The monkeys showed high frequencies of feeding 08.00 – 12.00 hr and 15.00 – 1800 hr. For drinking, a single peak from 12.00 – 13.00 hr emerged, after the morning peak of feeding.

Patas foraged mainly on the ground (36 of 54 encounters), and their faeces contained many grasshoppers (Orthoptera: Caelifera) that were abundant in the grass. Other remains found, of insect larvae, a hemipteran and a mantis, may have been prey taken from bushes or trees. Grass seeds appeared to be eaten but were not identified in faeces. Patas ate the leaves, buds, flowers, or fruits of 11 species of trees and large bushes at Assirik. Fruits not seen to be eaten by patas were found mainly in gallery forest or in woodland.

When approaching a waterhole, patas moved cautiously, and only one or two individuals usually drank at a time, while the rest waited nearby on rocks or in bushes. Similar caution occurred while drinking: short bursts of lapping were interspersed with looking around in vigilance. Once, a group of eight patas took 6 min for all members to drink and leave. Often the monkeys spent about half an hour idling in nearby trees after drinking. Even in the dry season, there were probably several waterholes (all natural) within the day-range of patas groups. Patas were seen 18 times on 11 days to drink at the waterhole near camp, over 17 days spent monitoring it.

Habitat Use

Observers were asked to record vegetation types as short-grass plateaux, tall grassland, deciduous woodland, or gallery forest. Patas were more often seen on plateaux, while green monkeys predominated in woodland and forest (Harrison 1983b). This difference was not explained by differential observability between the species.

The habitat where patas were most often encountered was an inter-gradation between plateau and woodland, although such a category was not in

the original coding system. Such transitional zones (ecotones) occurred between plateau and woodland but not between plateau and forest. Patas seemed to favour plateau/woodland edges, so, to cope with this complication, we created post hoc three further categories:

1. Ecotone: Plateau and woodland, where a graded, intermediate band of open bushland with scattered trees merged into intermixed open spaces and small belts or copses of trees.
2. Fringe: Woodland and plateau were well-defined and monkeys were seen close to the boundary, usually not more than 20 m into one habitat and never more than 100 m. Only short stretches of such well-defined fringe occurred in the study area.
3. Bushy marigot: Dry rocky beds of temporary streams crossing plateaux that often had scattered bushes and trees or strips of woody vegetation less than about 20 m wide.

Soon after the project finished, five SAPP members consulted field notes and applied independently and retrospectively this enlarged habitat classification to encounters with patas that they remembered well. When patas moved from one habitat to another, both data-points were used, but we kept the distinction between the first habitat recorded versus later ones. No differences existed across putative breeding groups, uncertain records, and all-male groups, so these data were pooled. First encounters ($n=160$) occurred most often in ecotone ($n=61$, 38%) and plateau (32.5%) habitats, followed by bushy marigot (13%) and woodland (11%). Few first sightings occurred in forest (3%) or fringe (2.5%). "Later" records ($n=80$), of when monkeys moved into another habitat type, showed woodland ($n=35$, 44%) as by far the most common habitat entered, followed by ecotone and plateau (each at 24%). Fringe (4%), bushy marigot (4%) and forest (1%) were almost never entered.

No evidence emerged that breeding groups normally penetrated beyond the edge of woodland. Five areas existed near camp where extensive woodland stretched for at least 800 m without a break. These areas were covered regularly by observers searching for chimpanzees or baboons. Only four times were breeding groups found to be more than about 200 m within such extensive woods. Patas at Assirik spent most of their time foraging and resting in ecotones between plateau and woodland or just within the woodland fringes. They made occasional forays across open plateaux

(where they were very conspicuous) and went into gallery forest only to drink or to use trees that were close to a plateau edge. They avoided areas of tall elephant grass, even after it had burned.

Group Composition

Groups of females with infants or juveniles usually were accompanied by one adult male ($n=79$ sightings), but twice two adult males were noted.

Sub-adult males sometimes were hard to distinguish from fully-grown females; we sometimes saw identifiable immature males in breeding groups but never more than one per group. Since juveniles (excluding dependent infants) often comprised half the membership of a breeding group, it seems likely that most males left their natal group before becoming strikingly different in appearance to females.

At least seven times, groups of three to five patas were seen to contain at least two adult males, with the others being confirmed subadult males. All-male groups usually behaved as a coherent unit, but sometimes individuals arrived and left in quick succession.

Lone males appeared regularly ($n=15$ sightings), but some of these apparently solitary males may have been associated with groups of females that were out of sight. Some may have been truly solitary, but several records of a lone male described an individual identical to the known male of a breeding group often seen near camp. Thus, it is likely that temporary separations (as noted above) between a group and its adult male may extend for longer periods. In 1979, we recorded female groups apparently lacking an adult male; these were concentrated in one area, suggesting that attachment between adult male and breeding group varies greatly.

Size of Breeding Groups

For this analysis, only records in which the observer had counted most (but not necessarily all) individuals were used. Infants carried ventrally were excluded. To avoid recounting the same group, the data first were separated into seven periods for which each period (usually centred on the early or late dry season) was separated from the rest by an interval without data. Then, in each period, the probable number of groups was calculated by using locality, distinctive features, and group size. Sets of data that differed in median group size by four or more members were taken to indicate different groups, as

were cases in which one record differed from a series by six or more individuals. This procedure yielded 26 “independent” breeding groups ranging in size from 7-28 (median = 13, with two-thirds of records = 10-22). Less restrictive criteria allowed one set of data to be assigned to two groups; this added six more units with a median of 12 and range of 5-28.

Overlap of Group Range and Overall Density

In the SAPP study area, patas seemed to move between localities at least 2 km apart. However, there was no reason to suspect regular interchange between the plateau around camp and another large plateau 4 km away, separated by at least 800 m of unsuitable habitat. Day-to-day patterns of encounters of groups during the two periods of intensive study strongly suggested that a group often spent several days in one part of its home range and then shifted to another part, although the monkeys easily could traverse the whole of the home range any day. Conservative estimates suggest that two or three groups regularly used the plateaux and open woodland within 700 m of camp. The groups rarely seemed to come into direct contact.

Thus, we tentatively estimated the density of the patas population in the best-monitored area, that is, within ca. 20 km² around camp. This area usually yielded a local population of 40-50 monkeys, with a minimum figure, over all four years, of 20. So, computed density in a sample area with typical proportions of all types of habitat ranged from 1-2.5 monkeys per km². The entire study area had about 625 ha of plateaux and open woodland (including ecotone between the two), so that densities in those combined habitat-types were about 3-8 km².

Within the SAPP study area, only one large plateau yielded no sightings of patas. It was the only one lacking surface water during the late dry season. To get to its nearest source of drinking water entailed crossing 500 m of elephant grass and scrub, then 1000 m across the next plateau.

DISCUSSION

The overwhelming conclusion from this limited and fragmentary data-set is the Assirik patas resemble those found further east in Africa (Isbell 2013). Repeatedly, our limited findings agree with those from Cameroon, Kenya and Uganda. This is reassuring, given that Assirik's patas appear to live in the most natural surroundings of any population studied so far, and that our data were collected opportunistically.

The ‘spaced-out’ dispersion and low frequency of sociosexual interaction found here echoes that noted at all other patas study sites (Hall 1965; Gartlan 1975; Isbell 2013). Similarly, the short, seasonal birth season is species-typical (Struhsaker & Gartlan 1970; Chism & Rowell 1988). Only the apparently high frequency of play, especially among adults, seems notable, and bears further investigation (but see Struhsaker & Gartlan 1970).

Few data have been presented on progression order in patas, but what we saw at Assirik seems to differ from elsewhere. At Laikipia, females typically initiated group movement and led progressions (Chism & Rowell 1988), whereas at Assirik, females were randomly placed in progressions. The widespread roving of a mixed sex group's adult male at Assirik resembles that seen elsewhere.

For relations with other species, most studies concentrate on patas and their potential predators. We found the same vigilance and alarm at large carnivores, but surprisingly little regard for jackals (cf. Gartlan & Gartlan 1973), which elsewhere prey on patas (Struhsaker & Gartlan 1970; Chism & Rowell 1988; Nakagawa 1999; cf. Burnham & Riordan 2012). Assirik patas never met the domestic counterpart of jackals, dogs (*Canis familiaris*), unlike elsewhere, where they kill patas (Chism & Rowell 1988; Enstam & Isbell 2004). As elsewhere, patas at Assirik distinguished between vervets and baboons, being tolerant of the former but wary of the latter (Hall 1965; Struhsaker & Gartlan 1970; Enstam & Isbell 2002). Assirik patas's responses to humans were like those elsewhere: they fled on the ground into cover, usually nearby woodland. Also, it seems to be a patas universal that much time is spent in vigilant scanning, often from elevated vantage points (Hall 1965; Gartlan & Gartlan 1973; Enstam & Isbell 2004).

Relations with ‘savannah monkeys’ (*Cercopithecus/Chlorocebus* spp.) seem to be peaceful everywhere that the two species coincide (Struhsaker & Gartlan 1970; cf. Gartlan & Gartlan 1973; Pruetz & Marshack 2009). This holds despite the fact that their dietary ranges overlap greatly, but inter-species competition seems to be ameliorated by their different habitat and food preferences, as studied in detail elsewhere (Nakagawa 1999). Harrison (1983a) showed that every plant taxon exploited by patas also was eaten by green monkeys; thus, any ecological segregation between the species was likely to be quantitative, not qualitative.

Only in southeastern Senegal are patas sympatric with chimpanzees. We saw no contacts between the two species at Assirik (McGrew *et al.* 2014), but

at nearby Fongoli the predator-prey relationship is clear, as chimpanzees prey on patas (Pruetz & Marshack 2009). At Assirik we saw patas and chimpanzees use the same waterhole on the same days, but at different times.

Patas everywhere seem to be relatively quiet (Hall 1965; Gartlan & Gartlan 1973), and Assirik's population is no exception. None of the calls that we heard at Assirik was unique (for our 'squeal', see 'scream-squeal' at Waza, Gartlan & Gartlan 1973; for our 'growl', see 'nyow' call and 'bark-grunt' at Laikipia, Enstam & Isbell 2002).

Patas diet seems to be much the same everywhere, emphasising insects and reproductive plant parts, such as fruit or seeds (Hall 1965; Nakagawa 1989, 1999, 2000, 2003; Isbell 1998). The importance of grass in the patas diet is unclear, being largely absent in some populations but more important elsewhere (Hall 1965). At Kala Maloue, patas harvested insect larvae from grass stems (Nakagawa 1999). Daily rhythms in feeding and drinking resembled those of patas elsewhere (Hall 1965; Nakagawa 1989).

Patas seem to drink every day if possible (Gartlan 1975; Nakagawa 1999), but some studies never saw drinking, even over many days of observation (Hall 1965). Gartlan (1975) reported multiple deaths from dehydration, when waterholes dried up. Some studies are complicated by the availability of artificial water sources, especially stock tanks (Isbell & Chism 2007; Burnham & Riordan 2012); even natural waterholes may be improved by human excavation (Struhsaker & Gartlan 1970). At Assirik, the saving grace for the patas are the steep-sided, narrow gorges formed by erosion of faults in the laterite plateaux; these offer year-round water long after exposed areas have dried out. These water sources are the reason that patas venture into closed canopy gallery forest, as otherwise these areas are avoided (cf. similar recessed water source amongst boulders, Chism & Rowell 1988). Patas at Laikipia avoid forested areas, which present the highest risk of encountering leopards, but sometimes the need for water overrides this preference (Burnham & Riordan 2012). We saw none of the crowded, multi-species aggregations at waterholes that were commonplace at Waza (Struhsaker & Gartlan 1970).

At Assirik, vegetation types intermediate between grassland and woodland seem to be favoured by patas, especially ecotone at plateau edges. Grassland at Assirik comes in two forms: tall, dense, monospecific stands of 'elephant grass' in low-lying basins are avoided, while swathes of short (< 75 cm tall) grass on plateaux are not. Plateau grassland is easily scanned by going bipedal (Enstam

& Isbell 2004). Penetration into woodland seems to be minimal, temporary and largely enforced by disturbance. Closed-canopy forest seems to be avoided everywhere by patas (Hall 1965; Chism & Rowell 1988; Nakagawa 1999; Enstam & Isbell 2002). Overall, the driving force behind patas monkey habitat use seems to be carnivore predation, perhaps especially from leopards in forest (Enstam & Isbell 2002, 2004; Burnham & Riordan 2012).

Social organisation of Assirik patas mirrors that found elsewhere: one-male-multi-female breeding groups, all-male groups of adults and subadults, and solitary adult males (Hall 1965; Gartlan & Gartlan 1973; Chism & Rowell 1986; Nakagawa 1999; cf. Ohsawa 2003). In both East and Central Africa, males immigrate into groups during the breeding season (Chism & Rowell 1986; Ohsawa *et al.* 1993), but we had too few data to corroborate this at Assirik.

Assirik's breeding groups were smaller than the averages elsewhere, at 12/13 members (Hall 1965; Struhsaker & Gartlan 1970, Galat-Luong *et al.* 1994; cf. Nakagawa 1999; Enstam & Isbell 2002; Isbell & Chism 2007), as was the upper range of sizes (Struhsaker & Gartlan 1970; Galat-Luong *et al.* 1994). Size and age-class composition of all-male groups was as elsewhere (Gartlan & Gartlan 1973; Gartlan 1975; Galat-Luong *et al.* 1994). Population density is hard to calculate in a mosaic habitat, but both figures computed here fall within patas norms elsewhere.

All in all, we found that Assirik patas are much like their counterparts in East and Central Africa. Only longer-term detailed study of habituated monkeys that can be followed all day at Assirik will reveal if some of the differences noted here, such as in progression order, interaction with jackals, small group size, are real or not.

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LITERATURE CITED

- Burnham, D. & P. Riordan. 2012. Avoidance of mammalian predators by patas monkeys (*Erythrocebus patas*) in a risky environment. *Folia Primatologica* 83(3-6): 288-298.
- Chism, J. & T.E. Rowell. 1986. Mating and residence patterns of male patas monkeys. *Ethology* 72(1): 31-39.
- Chism, J. & T.E. Rowell. 1988. The natural history of patas monkeys. In *A Primate Radiation: Evolutionary Biology of the African Guenons*. A. Gautier-Hion, F. Bourliere, J.-P. Gautier & J. Kingdon, eds. Cambridge University Press, Cambridge. Pp. 412-438.
- Enstam, K.L. & L.A. Isbell. 2002. Comparison of responses to alarm calls by patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in relation to habitat structure. *American Journal of Physical Anthropology* 119(1): 3-14.
- Enstam, K.L. & L.A. Isbell. 2004. Microhabitat preference and vertical use of space by patas monkeys (*Erythrocebus patas*) in relation to predation risk and habitat structure. *Folia Primatologica* 75(2): 70-84.
- Galat-Luong, A., F. Bibollet-Ruche, X. Pourrut, J.P. Durand, P. Sarni, G. Pichon & G. Galat. 1994. Social organization and SIV sero-epidemiology of a patas monkey population in Senegal. *Folia Primatologica* 63(4): 226-228.
- Galat-Luong, A. G. Galat, J.-P. Durand & X. Pourrut. 1996. Sexual weight dimorphism and social organization in green and patas monkeys in Senegal. *Folia Primatologica* 67(2): 92-93. (Abstract)
- Gartlan, J.S. 1975. Adaptive aspects of social structure in *Erythrocebus patas*. In *Proceedings of the Fifth Congress of the International Primatological Society*. S. Kondo et al., eds. Japan Science Press. Pp. 161-171.
- Gartlan, J.S. & S.C. Gartlan. 1973. Quelques observations sur les groupes exclusivement males chez *Erythrocebus patas*. *Annales de la Faculte des Sciences du Cameroun* 12: 121-144.
- Hall, K.R.L. 1965. Behaviour and ecology of the patas monkey, *Erythrocebus patas*, in Uganda. *Journal of Zoology* 148(1): 15-87.
- Harrison, M.J.S. 1983a. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. *Animal Behaviour* 31(4): 969-977.
- Harrison, M.J.S. 1983b. Patterns of range use by the green monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. *Folia Primatologica* 41(3-4): 157-179.
- Isbell, L.A. 1998. Diet for a small primate: insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). *American Journal of Primatology* 45(4): 381-393.
- Isbell, L.A. 2013. *Erythrocebus patas* Patas monkey (Hussar Monkey, Nisnas). In *Mammals of Africa. Volume II. Primates*, T.M. Butynski, J. Kingdon & J. Kalina, eds. Bloombury Press, Pp. 257-264.
- Isbell, L.A. & J. Chism. 2007. Distribution and abundance of patas monkeys (*Erythrocebus patas*) in Laikipia, Kenya, 1979-2004. *American Journal of Primatology* 69(11): 1223-1235.
- McGrew, W.C. 2014. Encountering crocodiles while chasing chimpanzees. *Pan Africa News* 21(1): 2-3.
- McGrew, W.C., P.J. Baldwin & C.E.G. Tutin. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution* 10(3): 227-244.
- McGrew, W.C., P.J. Baldwin, L.F. Marchant, J.D. Pruetz & C.E.G. Tutin. 2014. Chimpanzees (*Pan troglodytes verus*) and their mammalian sympatriates: Mt. Assirik, Niokolo-Koba National Park, Senegal. *Primates*, DOI: 10.1007/210329-014-0434-2
- McGrew, W.C., L.F. Marchant & C.A. Phillips. 2009. Standardised protocol for primate faecal analysis. *Primates* 50(4): 363-366.
- Nakagawa, N. 1989. Activity budget and diet of patas monkeys in Kala Maloue National Park, Cameroon: A preliminary report. *Primates* 30(1): 27-34.
- Nakagawa, N. 1999. Differential habitat utilization by patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) living sympatrically in northern Cameroon. *American Journal of Primatology* 49(3): 243-264.
- Nakagawa, N. 2000. Foraging energetics of patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*): Implications for reproductive seasonality. *American Journal of Primatology* 52(4): 169-185.

- Nakagawa, N. 2003. Differences in food selection between patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) in Kala Maloue National Park, Cameroon, in relation to nutrient content. *Primates* 44(1): 3-11.
- Ohsawa, H. 2003. Long-term study of the social dynamics of patas monkeys (*Erythrocebus patas*): group male supplanting and changes to the multi-male situation. *Primates* 44(2): 99-107.
- Ohsawa, H. M. Inoue & O. Takenaka. 1993. Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates* 34(4): 533-544.
- Pruetz, J.D.E. 2009. *The Socioecology of Adult Female Patas Monkeys and Vervets in Kenya*. Pearson/Prentice Hall, Upper Saddle River, NJ.
- Pruetz, J.D. & J.L. Marshack. 2009. Savanna chimpanzees (*Pan troglodytes verus*) prey on patas monkeys (*Erythrocebus patas*) at Fongoli, Senegal. *Pan Africa News* 16(2): 15-17.
- Sharman, M.J. 1981. Feeding, ranging and social organization of the Guinea baboon. PhD thesis, University of St. Andrews, Scotland.
- Struhsaker, T.T. & J.S. Gartlan. 1970. Observations on the behaviour and ecology of the patas monkeys (*Erythrocebus patas*) in the Waza Reserve, Cameroon. *Journal of Zoology* 161(1): 49-63.

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