



**An experimental demonstration of the impact of predation
on sexual segregation and primary sex ratios amongst
ungulates**

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1 **An experimental demonstration of the impact of**
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3 **amongst ungulates**
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21

22 Abstract

23 Underlying mechanisms of sexual segregation amongst ungulates, and Trivers and
24 Willard's hypothesis that mothers can influence primary sex ratios, continue to be topical
25 theoretical issues. Over two years, using monthly repeated road transects, we determined
26 the habitat and social segregation of male versus female impala (*Aepyceros melampus*)
27 and kudu (*Tragelaphus strepsiceros*) in a predator-free, versus a predator-laden, South
28 African reserve. We also determined, by the same technique but over four years, the
29 primary sex ratio of the impala population free from predation. Significant overlap in
30 habitat usage (Schoener's Index 0.63 to 0.8) was found between the two sexes when free
31 from predation, but not (Schoener's Index 0.46 to 0.47) when under predation. Whilst
32 occupying the same habitats impala, kudu and wildebeest (*Connochaetes taurinus*) male
33 and female groups maintained rigid social segregation throughout the year, even when at
34 close quarters. Impala primary sex ratios were significantly biased towards females
35 (male/female = 0.72; $\chi^2 = 4.3175$, df = 1, p-value = 0.038) in the absence of predation.
36 Our findings suggest that whilst risk of predation is a proximal cause of sexual
37 segregation, thus lending support to the predator-risk hypothesis, the underlying,
38 functional mechanism of sexual segregation is difference in the activity budgets of males
39 versus females (the activity-budget hypothesis). Our findings also suggest that mothers
40 may indeed be able to adjust primary sex ratios, with the postulated driver in this case
41 being an abnormally high density of adult males.

42

43 **Key Words:** bachelor herds, breeding herds, herbivores, reproductive strategy, savanna,
44 territorial
45

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Introduction

Sexual segregation

Three main hypotheses are generally discussed in the literature (Conradt 1997; Gross 1998; Main 1998; Main *et al.* 1996; Ruckstuhl and Neuhaus 2002) to explain sexual segregation. The forage-selection hypothesis (Beier 1987) suggests that females will select habitat based on food quality, while males should prefer high forage biomass, the predator-risk (or reproductive-strategy) hypothesis (Bowyer 1984) suggests that females will use relatively predator-safe habitats, while males are predicted to use habitats with higher predation risk but better food quality, and the activity-budget hypothesis (Conradt 1998) suggests that with increasing dimorphism in body size males and females will increasingly differ in the time spent in different activities.

The scramble competition hypothesis, forwarded as a variant of the forage-selection hypothesis, implies that females graze the vegetation in high-quality forage habitats too low for males to achieve sufficient forage intake rates, and males are thus forced by indirect female competition into marginal habitats with lower forage quality but higher forage biomass (Clutton-Brock *et al.* 1982; Clutton-Brock *et al.* 1987). This ‘indirect-competition’ hypothesis effectively extends Jarman’s (1974) and Bell’s (1971) argument for explaining inter-specific competition between different sized herbivore species to intra-specific competition between different sized sexes of the same species. However, removal of female red deer (*Cervus elaphus*) on the Isle of Rum, Scotland did not result in males increasing their use of preferred habitat as predicted by the hypothesis (Conradt *et al.* 1999), leading researchers to conclude that sex differences in body size

within a species are, in spite of theoretical considerations (Illius and Gordon 1992), not large enough for the Jarman-Bell principle to apply and, consequently, the hypothesis was rejected. Reviewing the literature on sexual segregation, Main *et al.* (1996) concluded that most evidence supported the reproductive-strategy hypothesis, whilst in a later and more extensive review Ruckstuhl and Neuhaus (2002) showed that there is considerably more evidence supporting the activity-budget hypothesis – out of 23 studies, 22 confirmed the predictions of the hypothesis.

Earlier studies often did not make clear whether they were discussing habitat segregation or social segregation or both, leading to confusion in the literature over the definition of sexual segregation (Main *et al.* 1996), with some studies discussing habitat segregation between the sexes (Tierson *et al.* 1985) whilst others discuss sexual segregation in terms of separation between sexes occupying the same habitat/area (McCullough *et al.* 1989). It is important that the type of sexual segregation being discussed is defined. Further confusion occurs over the near avoidance of the role of territoriality. This is probably because most field studies on sexual segregation have been carried out in northern temperate regions (Bleich 1993; Clutton-Brock *et al.* 1987; Main and Coblentz 1990; Miquelle *et al.* 1992) where territoriality is confined to a short, pronounced rut – sexual segregation occurring outside of the rut is thus not related to territoriality. This is not the case with several prevalent African ungulates – wildebeest (*Connochaetes taurinus*) maintain territories all year round except in the depths of winter (Attwell 1977), whilst zebra (*Equus burchelli*), although not defending an actual territory, vigorously repel other adult males from their harems all year round (Smuts 1974; 1976). In such cases clearly the behaviour of the dominant male keeps the bachelor groups

separate from the breeding herds and is the proximal cause of sexual segregation, whether with concomitant habitat segregation (wildebeest) or without (zebra). However, once territoriality stops, it is the persistence of sexual segregation, as also occurs in the northern hemisphere cervids, which is the interesting puzzle.

Over a two year period we determined in a predator-free game reserve, Ithala Game Reserve, South Africa, the habitat occupancy and social groupings of adult male and female wildebeest, impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*). An impala territorial male lives amongst its breeding herd all year round, but vigorously excludes other adult males, which live in bachelor herds, only during the pre-rut and rut (Jarman and Jarman 1973). Kudu do not show territoriality at all (Owen-Smith 1984a; b; Perrin 1999), but do show habitat segregation between the sexes over the calving and post-natal period (du Toit 1995). We also determined the same parameters, over two years, for impala and kudu in nearby Hluhluwe-iMfolozi Park – a reserve with similar habitats and climate to Ithala, but one with a full suite of predators (although few wildebeest). We assess our results here in terms of the three competing hypotheses on sexual segregation, noting that only the activity-budget hypothesis allows for social separation without concomitant habitat segregation, whilst the predator-risk hypothesis implies differing behaviour in the presence versus absence of predation.

Primary sex ratios (sex ratios at birth)

Fisher (1930) showed that natural selection favours those parents who invest equally in their male and female offspring. Trivers and Willard (1973) later argued that, under certain well defined conditions, natural selection favours deviations away from a 50/50

ratio but that these deviations cancel out in the local breeding population. They hypothesised that mothers in comparatively better condition would gain from a reproductive strategy where they biased the production of their young towards males, whilst those in a comparatively poorer condition would bias production towards females – the reasoning being that the condition of the young tends to correlate with that of the mother during the period of parental investment, and male offspring in superior condition are reproductively more successful, due to intra-sexual competition, whilst female offspring tend to reproduce whatever their condition. At the time Trivers and Willard hypothesised that such a bias might be effected by the female adjusting either the birth sex ratio or maternal investment after birth. In ungulates evidence for the former is equivocal and, rather, supports the latter (Hewison and Gaillard 1999). Recent results from the long-term study of red deer on the Isle of Rum, Scotland suggest that even post-weaning maternal associations affect the survival of offspring (Andres *et al.* 2013). Evidence for the Trivers and Willard hypothesis has also been put forward in relation to insects (Aron 2012), birds (Alonso-Alvarez 2006) and humans (Hopcroft and Martin 2014; Ruckstuhl *et al.* 2010), although its theoretical basis continues to be questioned (James 2013; Schindler *et al.* 2015).

Since, as Trivers and Willard emphasised (Hewison *et al.* 2002; Saltz 2001; Saltz and Kotler 2003), it is not environmental conditions *per se* which are predicted to influence the primary sex ratio but rather individual maternal condition *relative* to that of other mothers in the population, the overall primary sex ratio of a local population should be unaffected by environmental conditions and at parity. However, the Trivers and Willard hypothesis requires that a mother be able to assess her condition relative to those

mothers around her, so as to adopt the best reproductive strategy during that breeding season. If such ability is accepted as theoretically possible, it seems reasonable to propose additional abilities of mothers to assess other aspects of their local population with regards to parental investment decisions. Amongst African ungulates absence of predation can distort adult sex ratios, resulting in an abnormally large number of adult males (Berger and Gompper 1999; Dasmann and Mossman 1962; O'Kane and Macdonald 2015; Vincent 1979). We propose it would benefit mothers to invest more heavily in daughters if, in the absence of predators differentially reducing the number of males reaching sexual maturity, considerable numbers of sons were unable to gain access (by establishing territories) to reproductive females i.e. were surplus, functionally, to requirements.

We previously determined (O'Kane and Macdonald 2015) that the adult male to female ratio amongst impala, a ubiquitous African ungulate, in predator-free Ithala Game Reserve is indeed unusually male heavy (adult male/female = 0.69), when compared to reserves with predators (e.g. Hluhluwe-iMfolozi Park = 0.43 (O'Kane and Macdonald 2015), Hwange = 0.42 (Anderson 1967), Fort Tuli = 0.45 (Dasmann and Mossman 1962)). Over a four year period we determined the primary sex ratio of impala in Ithala Game Reserve, hypothesising that the ratio would not be at par but bias towards females.

Methods

Study areas

161 Ithala Game Reserve (29,653 ha) is situated in northern KwaZulu Natal, South Africa
162 (27°30'S, 31°25'E). Elevation ranges from 350 to 1550 m a.s.l. Long-term annual rainfall
163 is 791mm, falling mainly during the summer (October to March). Summers are warm to
164 hot (daily average of 18-30°C), with winters being warm to mild (15-25°C) (Porter
165 1983). The reserve is located in steep, dissected terrain, interspersed with broad grassy
166 plains. Geology includes Archaean granite exposures, sandstones, shales and mudstones
167 of the Karoo system, and igneous dolerite dykes and sills (Porter 1983). Correspondingly,
168 soil types are as varied, although shallow, rocky (lithosols) of the Mispah form
169 predominate (Turner 1980). The vegetation is a mix of Zululand central bushveld at mid-
170 elevations and Zululand lowveld bushveld at low elevations (Low and Rebelo 1996).
171 Structurally it is a mosaic of grasslands, open savanna dominated by *Acacias* and more or
172 less closed thickets of broad-leaved shrubs and trees.

173 Indigenous animal populations had largely been destroyed by the 1950's in the
174 reserve by a mixture of farming (since 1884), a rinderpest epidemic (1896) and hunting,
175 including that to control tsetse fly (1919-1950) (Johnson 1990). The Natal Parks Board
176 purchased the land in 1972 and stocked it with indigenous mammals typical of the south-
177 eastern African savanna, including warthog (*Phacochoerus aethiopicus*), impala, black
178 (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), zebra (*Equus burchelli*),
179 buffalo (*Syncerus caffer*), wildebeest, kudu, giraffe (*Giraffa camelopardalis*) and
180 elephant (*Loxodonta africana*). The reserve is entirely fenced except to the north where
181 animal movement is limited by the substantial Pongola River. Consequently no
182 significant immigration/emigration of animals occurs. The reserve does not contain (and
183 has not since foundation) any large mammalian predators and carries moderate densities

of impala (10 km^{-2}), but high densities of wildebeest (6 km^{-2}) and zebra (5.6 km^{-2}) (O'Kane et al. 2014).

Hluhluwe–iMfolozi Park (900 km^2) ($28^{\circ}00'–28^{\circ}26'S$, $31^{\circ}43'–32^{\circ}09'E$) is situated some 70kms from Ithala. It is completely fenced, with altitude ranging from 450 m to 60 m a.s.l. In iMfolozi, the section favoured by impala and kudu (O'Kane *et al.* 2013), long-term annual rainfall is 635mm and vegetation consists mainly of Zululand lowveld bushveld (Mucina and Rutherford 2006), characterised by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy. Soils are similar to those found in Ithala. The reserve carries a full suite of megaherbivores (elephant, rhino and giraffe) and mesoherbivores (impala, kudu, nyala, wildebeest, zebra) and considerable numbers of mammalian predators (lion, hyaena, cheetah, leopard and wild dogs). Impala exist at a high density of 26 km^{-2} (K.Z.N.Wildlife 2008).

Data collection

In Ithala Game Reserve and Hluhluwe–iMfolozi Park for two years (encompassing two wet and dry seasons) monthly, over a six day period, road transects covering a representative sample of the reserve's different vegetation types were carried out by the same observer. Transects were driven at the same time during each field trip, with midday avoided. Once within a classifiable distance ($< 50\text{m}$, using binoculars) with an unobstructed view of the individual/group of herbivores, the number (recording rapidly left to right) of wildebeest, impala and kudu, their age, sex and habitat occupancy were determined. The route of the chosen transects was such that animals counted on one transect would not have had time to move to another transect – thus double counting of

207 animals was unlikely. The precise criteria for age and sex classification are as in Brooks
 208 (1985); habitats were classified according to Balcomb (1996). The vegetation
 209 communities, or habitat types, may be described in more detail as follows, with plant
 210 nomenclature after Pooley (2003): (1) riverine and scree forest (continuous, riverine
 211 vegetation), (2) wetlands (sparse, wetland vegetation), (3) undulating tall grassland
 212 (sparse, old croplands not on flood plain, dominated by *Hyparrhenia* and *Hyperthelia* sp.
 213 with smaller areas of increaser grass species dominated by *Themeda triandra*; where
 214 woody species are present these include *Dichrostachya cinerea*, *Rhus lucida* and *Acacia*
 215 *nilotica*), (4) basin bushveld and thicket (closed, *Euclea racemosa*, *D. cinerea*, *A.*
 216 *nilotica*, *Faurea saligna*, *Euphorbia ingens* – sparse *F. saligna* and *E. ingens* < 2.5m in
 217 height), (5) mixed thornveld (ranges from open, through continuous to closed; disturbed
 218 lands, often old kraal sites, *A. nilotica*, *Aloe marlothii*, *Maytenus heterophylla* and
 219 *Dombeya rotundifolia*), (6) sparsely wooded hill slopes (open, *Combretum apiculatum*,
 220 *D. rotundifolia*, *M. heterophylla*, *A. nilotica* - *C. apiculatum* seldom found at heights <
 221 2.5 m), (7) tall deciduous woodland (closed, *Acacia nigrescens*, *A. tortilis*, *A. robusta*,
 222 *Spirostachys africana*, *Maytenus senegalensis*), (8) woody rocky outcrops (ranges from
 223 open to closed; patchy unit composed of grassland with granite outcrops on which woody
 224 species found include *Terminalia phanerophlebia*, *Sclerocarya birrea* subsp. *caffra*, *A.*
 225 *nilotica*, *Lannea discolor*).

226 Impala are seasonal breeders and, as previously observed (Brooks 1985), lamb in
 227 Ithala Game Reserve over a few weeks in November and December. Although only male
 228 impala carry horns, the window of opportunity for confidently assigning sex to all
 229 juveniles is small. In the months immediately following birth horn buds in the males,

once they appear, are only seen close up (leading to a bias in recorded males as this is the only sex one can, when occasionally close enough, assign), and by May female juveniles, due to their almost equal size, are difficult to distinguish from yearling females. Thus the sex of impala juveniles in Ithala Game Reserve was recorded only over March and April, with data being gathered over a four year period by the road transect method described above. By restricting the determination of impala juveniles' sex to these two months, virtually all (> 95%) juveniles spotted within the classifiable distance (< 50m, using binoculars) were sexed.

Data analysis

For impala we compared habitat usage of breeding herds versus bachelor herds over the period June to February (thus excluding the territorial pre-rut/rut period of March to April). For kudu we compared adult female versus adult male habitat usage over the calving/post-natal period of March to July with the rest of the year (August to February). For both species we then compared our findings in predator-free Ithala Game Reserve versus those in predator-heavy Hluhluwe-iMfolozi Park. Percentage overlap is the simplest measure of niche overlap to interpret because it is a measure of the actual area of overlap of the resource utilization curves (Krebs 1999). We assessed overlap in habitat usage between pairs of social groupings of a herbivore species using Schoener's index (Schoener 1970), recommended by Abrams (1980) as the best of the measures of niche overlap (Krebs 1999). Where there is no use of the same resources this index is zero, and where completely identical resources are used it is one; overlap is significant where the index ≥ 0.6 (Wallace 1981). Schoener's index for overlap of habitat usage was:

253
$$S_{ab} = 1 - \frac{1}{2} \sum_{i=1}^n |p_{ai} - p_{bi}|$$

254 where S_{ab} = Schoener's index for overlap of habitat usage between social groupings a and
255 b of a species, p_{ai} = proportion of the overall habitat usage that usage of habitat type i by
256 social grouping a forms, p_{bi} = similarly for social grouping b , n = number of habitat
257 types. Although Schoener's index is relatively unaffected by sample size (Krebs 1999),
258 too few wildebeest were recorded in Hluhluwe-iMfolozi Park for analysis. We also
259 assessed differences in the proportion of breeding herds/females occupying habitat types
260 not occupied by bachelor herds/males, between reserves or at different times of year, by
261 applying Pearson's chi-square test with Yates' continuity correction (Crawley 2005).

262 In southern Africa juvenile impala of both sexes remain within their natal herd
263 throughout the first year of life (Jarman and Jarman 1973; Murray 1982). We assumed
264 there is no significant difference in their mortality while both sexes remain within the
265 herd, and that therefore the juvenile sex ratio recorded over March and April equals the
266 primary sex ratio. We tested for significance ($P < 0.05$) of departures from parity in the
267 primary sex ratio by applying Pearson's chi-square test with Yates' continuity correction,
268 carried out in S-PLUS (MathSoft 1999).

269

270

271 **Results**

272

273 *Sexual segregation*

Wildebeest Ithala Game Reserve. The majority of wildebeest territorial males abandoned their territories over the height of the dry season, moving to join the breeding herds which were principally located on flushes of grass induced by winter burning. Over this period bachelor herds of wildebeest also joined the breeding herds on the grass flushes, but remained socially segregated from the females (Fig. 1).

Impala Ithala Game Reserve vs Hluhluwe-iMfolozi Park. Impala bachelor herds remained socially segregated from breeding herds throughout the year in both reserves. Even in the depths of winter when bachelors were observed to associate more closely with breeding herds, they maintained their group cohesion and were still clearly separate from the breeding females. Outside of the pre-rut/rut period, in both Hluhluwe-iMfolozi Park and Ithala Game Reserve a small proportion (~2%) of breeding herd females was seen to occupy habitat types not occupied by bachelor herds, with no significant difference ($\chi^2 = 1.893$, $df = 1$, $p\text{-value} = 0.1689$) between the two reserves. However during this period whilst there was a highly significant overlap (Schoener's index = 0.8) in habitat usage between breeding and bachelor herds in predator-free Ithala Game Reserve, there was no significant overlap (Schoener's index = 0.47) between the two groups in Hluhluwe-iMfolozi Park.

Kudu Ithala Game Reserve vs Hluhluwe-iMfolozi Park. Outside of the rut, adult male kudu maintained social segregation from adult females in both reserves. In predator-free Ithala Game Reserve, the proportion of adult female kudu observed in habitat types in which adult males were not observed was very low (0.5% to 2%), and there was no significant ($\chi^2 = 0.1358$, $df = 1$, $p\text{-value} = 0.7125$) difference in these proportions comparing the calving/post-natal period with the rest of the year. Additionally,

Schoener's Index revealed significant and similar degrees of overlap in habitat utilisation between adult male and female kudu when comparing the calving/post-natal period (Schoener's index = 0.64) with the rest of the year (Schoener's index = 0.68). However in Hluhluwe-iMfolozi Park, containing a full suite of predators, the proportion of adult female kudu observed in habitat types in which adult males were not observed was considerably higher (54% calving/post-natal period; 25% rest of the year), and there was a highly significant ($\chi^2 = 11.6104$, $df = 1$, $p\text{-value} = 0.0007$) difference in these proportions between the two periods. Moreover, there was no significant overlap in habitat utilisation between adult male and female kudu during the calving/post-natal period (Schoener's index = 0.46), whilst overlap was significant (Schoener's index = 0.63) over the rest of the year.

Primary sex ratios

We recorded more female than male impala juveniles, over the months of March and April, in each of the four years of the study (Year 1, female: male 26:22; Y2, 58:44; Y3, 33:21; Y4, 81:55). Overall, the number of female to male impala juveniles significantly departed from parity and was biased towards females (male/female = 0.72; $\chi^2 = 4.3175$, $df = 1$, $p\text{-value} = 0.038$).

Discussion

Sexual segregation

Attwell (1977), studying wildebeest in Hluhluwe-iMfolozi Park, also reported, as we found in Ithala Game Reserve, that when territorial bulls were not enforcing habitat segregation bachelor wildebeest joined the breeding herds on favoured grazing lawns, but maintained social segregation. Anderson (1972) recorded in Hluhluwe-iMfolozi Park that after territorial behaviour had declined (i.e. outside of the rut) impala bachelor herds maintained habitat segregation. Jarman (1972), working in the (predator-laden) middle Zambezi Valley, also recorded differential habitat selection by male versus female impala outside of the rut. Our findings in Hluhluwe-iMfolozi Park were similar but contrasted sharply with our findings in predator-free Ithala Game Reserve where, although social segregation was maintained throughout the year, we found extensive overlap in habitat usage between bachelor and breeding herds outside of the rut. Du Toit (1995), working in the Kruger, showed that whilst male and female kudu live in the same habitat during winter, over the calving and post-natal period they show habitat segregation, arguing that this results from females occupying habitats where their calves are less at risk from predation. Our results support du Toit's findings and argument, as in predator-laden Hluhluwe-iMfolozi Park kudu males showed significant habitat overlap with females outside of, but not during, the calving and post-natal period, whilst in predator-free Ithala Game Reserve the two groups showed significant and similar degrees of habitat overlap over both periods (i.e. the entire year). Perrin (1999) also reported the year round (apart from over the rut) social segregation between male and female kudu that we observed in both reserves.

Blumstein (2002) discussed antipredator behaviour and its retention/loss overtime in the absence of predation, arguing that costly antipredator behaviour should be lost if it

is no longer beneficial. He observed that visual predator recognition is strongly retained despite no exposure to predators, but that other behaviours (e.g. flight distance) are less 'hard wired' and are reduced over time in the absence of predators. Avoidance of habitats potentially carrying higher predation risk appears to be an example of a behavioural pattern rapidly discarded without exposure to predation. It would also be in accordance with various correlational studies (Greenwood 1980; Switzer 1995; 1997) that have shown that an individual's past reproductive success often increases its breeding site fidelity, suggesting that individuals use their reproductive experience to assess habitat quality. A mooted introduction of large predators into Ithala Game Reserve may provide a natural experiment in how quickly antipredator behaviour is reacquired, as well as providing further correlative evidence on the proximal role of predation in sexual segregation.

Our results thus suggest that when territorial behaviour no longer applies, predatory pressures may maintain habitat segregation between adult male and female ungulates, but where predation is absent, as in Ithala Game Reserve, although the two groups then demonstrate considerably less habitat segregation they rigidly maintain social segregation. Of the three hypotheses outlined in the introduction, only the activity-budget hypothesis allows for sexual segregation without concomitant habitat segregation. An attraction of the activity-budget hypothesis is that it provides a convincing functional explanation for the persistence of bachelor groups even when bachelors are not forced to remain as such – namely that differences in activity budgets would increase the costs of synchrony necessary to maintain group cohesion in a mixed sex group (Aivaz and Ruckstuhl 2011). Differing activity budgets are the most likely cause of sexual

segregation across a range of species (e.g. bats, Levin *et al.* 2013; penguins, Ludynia *et al.* 2013; and monkeys, Hartwell *et al.* 2014), whilst sexual segregation has been reported amongst monomorphic birds (Hedd *et al.* 2014) and monomorphic fish (Griffiths *et al.* 2014). Main *et al.* (1996) observed that the universal nature of sexual segregation among polygynous ungulates suggests this behaviour is the product of selective pressures from a similar evolutionary background and, moreover, that it would be more profitable to understand sexual segregation in terms of selective pressures that influence reproductive success across taxa, rather than to concentrate solely on separate species- or site-specific explanations. The varied causes of sexual segregation that our data point to reinforce Ruckstuhl's (2007) observation that different factors need to be integrated to successfully describe proximal and ultimate causes of sexual segregation. Furthermore, possible influences on sexual segregation other than the principal hypotheses assessed and discussed here have been variously proposed (e.g. parasite loads (Ferrari *et al.* 2010), environmental factors (Ruckstuhl and Neuhaus 2009), reproductive status, population density and sex ratios (Ruckstuhl *et al.* 2006)).

Primary sex ratios

Although we found a significant bias towards female juvenile impalas over the four year study, it should be born in mind that as we determined the 'primary sex ratio' up to six months after birth, causes other than differing maternal investment in male versus female juveniles (e.g. differing susceptibility to disease or resource availability) may be responsible. Nonetheless, given that in the study reserve impala juveniles of both sexes

389 remained within their natal herds over the first year of life and that predators are absent, it
390 is difficult to envisage what these other causes realistically might be. Our findings lend
391 support to the underlying hypothesis of Trivers and Willard (1973) that mothers possess
392 the ability to influence the primary sex ratio. However Trivers and Willard specifically
393 described the situation of mothers favouring a sex dependent on their condition in
394 relation to other mothers, whilst the overall local population primary sex ratio remains at
395 parity. Our finding of an overall local population primary sex ratio bias towards one sex
396 is different, as is our postulated driver of an unnatural excess of adult males consequent
397 on their reduced mortality in the absence of predation. If such a driver exists, it would
398 presumably be effected via an endocrinal response in females related to excessive
399 territorial aggression amongst the abnormal high density of adult males. Ideally in our
400 study we would have compared the primary sex ratio in predator-free Ithala Game
401 Reserve with that in predator-laden Hluhluwe-iMfolozi Park, expecting, if our postulated
402 driver exists, to record the primary sex ratio at parity in the latter. Interestingly, Schindler
403 et al. (2015) have recently attempted to extend and generalize the Trivers-Willard theory
404 to incorporate the different life-history traits of females and males in polygynous species.

405 Arguing against our postulated driver, lack of predation may translate into
406 stronger competition amongst adult males leading to a faster turnover of territories and/or
407 smaller territories; in such a case a mother would need to continue to produce her crop of
408 sons to enter into this increased competition and would not gain from favouring more
409 daughters. Although territory size appears to decrease with increasing overall population
410 density (Estes 1997), there appear to be no analyses in the literature of ungulate territory
411 size or time held in relation to density of adult males.

412

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588

Figure 1: Wildebeest bachelor herds as a percentage of the total adult wildebeest population in Ithala Game Reserve. During every field period of the two year study, including over the height of the dry season (July/August/September), bachelor herds were observed as socially segregated from breeding herds. The total adult population of wildebeest in the reserve was obtained from management’s annual census, whilst the crosses (first year) and triangles (second year) mark the months of the two years of data collection.

Figure 1

