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Does the activity budget hypothesis explain sexual segregation in ungulates?

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The activity budget hypothesis proposes that the main force driving sexual segregation is the difference in activity between males and females. Recently, a model was developed to demonstrate explicitly that such differences in activity could, in theory, produce sexual segregation (Ruckstuhl & Kokko 2002, *Animal Behaviour*, **64**, 909–914). The question remains whether realistic parameter values can also generate significant sexual segregation. Using this model and data on the body size dimorphism for 144 ungulate species, we compared the sexual segregation predicted by the model with expectations based on field observations. The results do not support the activity budget hypothesis as the main factor explaining sexual segregation. We investigated activity synchronization, the animal movement rule and transient spatial distributions in further detail. Introducing activity synchronization into the model slightly increases the ability of the activity budget to generate sexual segregation. Changing an animal's movement rule has a strong effect; movement rules that are independent of activity generate no long-term segregation. Finally, changes in a population's home range allow activity budget differences to generate transient sexual segregation. This method of generating sexual segregation is not sensitive to the animal movement rule and is potentially an important mechanism by which activity budgets can generate sexual segregation.

Most ungulate species that are sexually dimorphic in body mass live in separate groups outside their breeding season (Nowak 1999; Ruckstuhl & Neuhaus 2002). This widespread behaviour is known as sexual segregation. At present the underlying factors responsible for sexual segregation are poorly understood, but if these factors can be clarified it will inform our understanding of animal spatial distributions and the evolution of sociality. Sexual segregation can be due to differences in habitat preferences between males and females (Mysterud 2000), although the reasons for these habitat preferences are not well known. Habitat preference is not the complete explanation, however, because segregation is also seen within the same habitat. This type of segregation is known as social segregation and need not be limited to sexual segregation, since it can also occur between different cohorts of the same sex (Bon 1991; Bon & Campan 1996). For the rest of this paper we are concerned with segregation that is not due to habitat preferences, and for the most part we assume this segregation to be sexual segregation.

A variety of hypotheses have been proposed to explain sexual segregation in mammals (Main & Coblentz 1990; Main 1998). These hypotheses can be categorized into three main groups (Main et al. 1996): (1) the predation risk (or reproductive strategy) hypothesis states that females with offspring will choose predator-safe habitats even if this is at the expense of nutrient intake (Main & Coblentz 1996; Corti & Shackleton 2002), whereas males attempt to gain competitive supremacy and access to mates by accumulating reserves to invest in increasing body size (Clutton-Brock et al. 1982; Prins 1989); (2) the forage selection (or sexual dimorphism–body size) hypothesis states that allometric differences in body size, bite size and the efficiency of fibre digestion lead to different foraging efficiencies between the sexes and consequently to differences in habitat use that could promote sexual segregation (Demment 1982; Clutton-Brock & Harvey 1983; Demment & Longhurst 1987; Illius & Gordon 1987; Barboza & Bowyer 2000); and (3) the social factors hypothesis states that males and females differ in their ontogenetic behaviour, resulting in different levels of activity and patterns of interaction, leading to a social autosegregation by sex–age classes (Bon & Campan 1996). So far none of these hypotheses has provided a satisfactory, general explanation of sexual segregation in ungulates.

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One further hypothesis, the activity budget hypothesis, has been recently proposed and has received special attention in the literature (Ruckstuhl 1998, 1999; Ruckstuhl & Neuhaus 2000, 2001, 2002; Neuhaus & Ruckstuhl 2002; Michelena et al. 2004). This hypothesis (Ruckstuhl 1998) proposes that segregation arises from the difference in time spent active between males and females. The hypothesis is based on two main assumptions (Ruckstuhl & Neuhaus 2002): (1) females are less efficient at digesting forage than males, owing to body size digestive constraints (i.e. smaller stomach and shorter passage rate of the food through the digestive system, Demment 1982; Robbins 1993), and (2) big differences in activity budgets make synchrony of behaviour difficult and possibly costly (Conradt 1998a; Conradt & Roper 2000, 2003). The predictions of this hypothesis are: (1) smaller animals will compensate for their lower digestive efficiency by foraging for longer, whereas larger animals will spend more time ruminating or lying; (2) groups will be formed by animals with similar activity budgets (Ruckstuhl & Neuhaus 2002). Since the hypothesis is based upon differences in body size rather than sexual differences, it predicts segregation between cohorts of the same sex as well as sexual segregation.

The activity budget hypothesis was formalized into a model by Ruckstuhl & Kokko (2002) to demonstrate that differences in activity budget can, in theory, give rise to realistic degrees of sexual segregation without same-sex preference, opposite-sex aversion or any other socially related factors. Models such as this provide a quantitative estimate of the sexual segregation to be expected from a difference in activity budgets. Although the model of Ruckstuhl & Kokko successfully demonstrates sexual segregation with theoretical parameter values, the question remains whether realistic parameter values can also generate significant sexual segregation. We examined this question by using data from 144 ungulate species to parameterize their model. We investigated the robustness of their model, and explored extensions of the model which allow for activity synchronization, changes in a population's home range and transient effects following such a change (e.g. following aggregation resulting from the breeding season).

THE ACTIVITY BUDGET MODEL APPLIED TO UNGULATE SPECIES

We reconstructed the individual-based model by Ruckstuhl & Kokko (2002) using MATLAB (programs available from J.M.Y.). For a detailed description of the model see Ruckstuhl & Kokko (2002). The model considers an equal number of male and female animals in a square, homogeneous environment (each side is defined as one unit in length). Each animal can be in one of two states: active (i.e. moving) or inactive (i.e. stationary). The activity budget of an animal is quantified by the probability per time step of switching state from inactive to active (p_m for males and p_f for females) and from active to inactive (q_m for males and q_f for females). Following Ruckstuhl & Kokko, p_m and p_f are called the propensity to switch, and they are chosen to be inversely related, such that

$p_m = 0.01 - p_f$. The propensity to switch, p_f, is also chosen to be inversely related to q_f such that $p_f + q_f = 0.01$, and similarly for males. Ruckstuhl & Kokko (2002) found that noninverse relationships weakened the sexual segregation. If an animal is active then it moves a distance s every time step. This movement is in a random direction if no active animal is within a distance d, otherwise the focal animal moves at random within a segment of $120°$, centred on the nearest active animal.

We parameterized Ruckstuhl & Kokko's model (2002) for Scottish red deer stags, *Cervus elaphus*, details of which are given in the Appendix and in Table 1. Sexual segregation was measured by the probability of an individual having a nearest neighbour of the same sex. This provides a measure of segregation for males and females that is unbiased because the model contains an equal number of males and females. In cases where the sex ratio differs from unity, or the population density or group sizes vary, the segregation coefficient should be used to give an unbiased estimate of segregation (Conradt 1998b, 1999). Figure 1 shows a typical example of the animal distributions generated by the model. The model was initially used to reproduce successfully the results of Ruckstuhl & Kokko (Fig. 2), which showed that substantial sexual segregation can be generated provided there is a sufficient difference between the activity budgets of the two sexes. Figure 2 also shows that the more active sex (females) tends to be more clustered under the assumptions of the model. This is verified by looking at the mean distance to the nearest neighbour ± SD which is 0.015 ± 0.001 for the more active sex (females) and 0.032 ± 0.004 for the less active sex (males). These nearest-neighbour distances appear to be too large for red deer, because for Scottish red deer a group is usually defined by a separation greater than 50 m, which corresponds to a nearest-neighbour distance of 0.0036 (Clutton-Brock et al. 1982). Reducing the model's time step by a factor of 10 (240 time steps per day) gives a nearest-neighbour distance of about 0.0025,

Table 1. The default parameter values used in the model

Parameter	Value
Number of males	50
Number of females	50
Size of model arena	1×1
Movement step size per iteration, s	0.015
Probability of conforming, c	0
Maximum nearest-neighbour distance, d	1
Error in animal movement, $\theta°$	+/−60
Probability per time step of switching state	0.01
Length of a simulation (days)	200
Time steps per day	24

The model has one variable: the propensity to switch state, p_f, which is the probability per time step that a female switches from being inactive to active. The probability per time step that a female switches from being active to inactive, q_f, was chosen following Ruckstuhl & Kokko (2002) so that $p_f + q_f = 0.01$, and the probability that a male switches state is given by $p_m = q_f$ and $q_m = p_f$. The activity ratio, α, is related to the propensity to switch through the equation, $\alpha = p_f/p_m$. All values are identical to those given by Ruckstuhl & Kokko (2002), with the exception of s, which is parameterized from data on red deer (Sibbald et al. 2001).
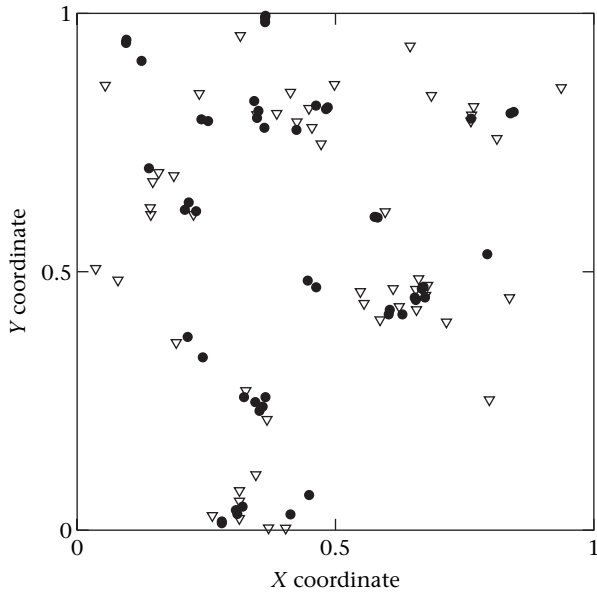
Figure 1. The final spatial distribution of males ($\triangledown$) and females ($\bullet$) from one realization of the model when $p_f = 0.008$.

but has no significant effect upon the level of sexual segregation. A realistic model should also predict realistic group sizes.

An important point is the type of segregation generated by the model. We measured segregation by the probability of an individual having a nearest neighbour of the same sex. This measurement is insensitive to the spatial distribution of the animals. Intuitively, as segregation
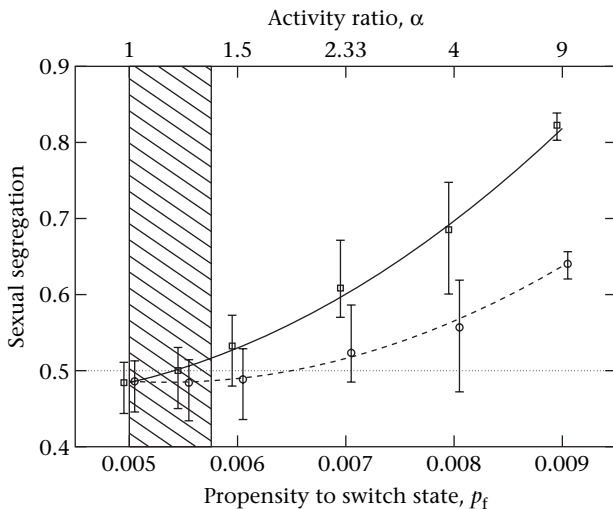

Figure 2. Sexual segregation predicted from the reconstructed model and equivalent to Figure 1 in Ruckstuhl & Kokko (2002). Activity ratio has been added as a second X axis to compare with propensity to switch state. Solid and dashed lines are the best-fit quadratic regression lines for females and males, respectively. Error bars show the range of data from 10 runs of the model, the mean value is indicated by the marker, the range of activity ratios calculated in Table 2, for strongly segregating species, is shown by the hatched region, and the horizontal dotted line shows the case where no sexual segregation is present. For clarity the values along the X axis for males and females have been slightly displaced.

increases (Fig. 2), we predict the emergence of two well-defined groups of individuals, with a significant spatial separation between the centroids of the two groups. However, in the activity budget model the spatial distribution of males and females is sympatric, with small groups of the same sex spread across the entire virtual arena (Fig. 1).

The sexual segregation generated by the model depends upon the sexual difference in activity budgets. This raises the question of how large are the differences in activity budgets for segregating species. To address this question, we classified male and female body masses from a comprehensive list of 144 ungulate species (Pérez-Barbería & Gordon 2000) into three groups according to their observed segregation outside the breeding season: no segregation, mixed groups temporarily segregated and segregation (Myslenkov & Voloshina 1998; Nowak 1999; Ruckstuhl & Kokko 2002; Ruckstuhl & Neuhaus 2002; M. Krasinska, personal communication; J. T. Du Toit, personal communication). The sexual difference in activity budget was quantified by an activity ratio, α, which estimates the feeding time necessary to meet maintenance requirements for the more active sex relative to the less active sex (Table 2, details of the calculation are given in the Appendix). Figure 3 shows the relation between body size dimorphism and activity ratio for two allometric exponents of feeding rate against body mass. Since this relation predicts an activity ratio greater than one for the majority of species, we assume from now on that females are the more active sex (although the model also predicts sexual segregation when males are more active). For the rest of this paper we also assume that feeding rate is proportional to body mass, because this scaling predicts the largest range of activity ratios (Fig. 3) and is more consistent with the data on grazing activity (Ruckstuhl & Neuhaus 2002). Activity budgets may be affected by factors other than maintenance requirements, and field observations of activity budgets may account for these other factors. For example, Ruckstuhl (1998) observed bighorn sheep, *Ovis canadensis*, for 8–14-h periods between April and September and found activity ratios in the range of 1.08–1.39 (compared to our estimate in Table 2 of 1.11). However, obtaining a reliable estimate of the average activity budget for each sex over the year is complicated, because of the different energy requirements that each sex has across the seasons. In the model, the activity ratio is related to the propensity to switch state via the formula $p_f = 0.01\alpha/(1 + \alpha)$. For those species that show strong segregation (Table 2), the activity ratio ranges from $\alpha = 1$ to $\alpha = 1.357$ ($p_f = 0.005$–0.0058, this range is shown in Fig. 2 by the hatched region). The fit of the activity budget model is poor (Fig. 2) because over the range of realistic activity ratios the predicted sexual segregation is lower than that expected for this group of strongly segregating species. A precise quantitative comparison between these predicted values and the segregation observed in the field is difficult because most of the information available in the literature is qualitative (Conradt 1998b; Mysterud 2000). Nevertheless, our statement that the predicted segregation (maximum probability of a same-sex neighbour about 0.6) is lower than those

Table 2. The average annual body mass, maintenance requirement and activity ratio (both corrected and uncorrected for intake, see Appendix) for a range of large ungulate species

Species	Sexual segregation	Body mass (kg)		Maintenance requirement (kg dry mass/day)		Activity ratio, α (Female:Male)	
		Male	Female	Male	Female	Feeding rate ∝ $BM^{0.71}$	Feeding rate ∝ $BM^{1.0}$
Addax nasomaculatus	2	117.67	84.67	1.29	1.03	1.01	1.11
Aepyceros melampus	2	56.91	43.76	0.74	0.62	1.00	1.08
Alcelaphus buselaphus	2	152.06	144.59	1.58	1.52	1.00	1.02
Alcelaphus lichtensteini	2	178.31	162.71	1.78	1.67	1.00	1.03
Alces alces	2	510.15	358.80	4.02	3.19	1.02	1.13
Ammodorcas clarkei	1	30.64	25.43	0.46	0.40	1.00	1.06
Ammotragus lervia	2	111.83	51.60	1.24	0.74	1.03	1.28
Antidorcas marsupialis	2	40.68	35.55	0.57	0.52	1.00	1.04
Antilocapra americana	1	56.24	49.84	0.73	0.67	1.00	1.04
Antilope cervicapra	1	40.16	34.37	0.57	0.51	1.00	1.05
Axis porcinus	2	44.12	30.61	0.61	0.47	1.00	1.12
Bison bison	2	795.25	452.83	5.68	3.95	1.04	1.22
Bison bonasus	2	718.00	423.00	5.24	3.72	1.03	1.20
Blastocerus dichotomus	2	140.00	120.00	1.48	1.33	1.00	1.05
Bos gaurus	2	848.39	701.90	5.97	5.27	1.01	1.07
Bos grunniens	2	590.50	306.00	4.50	2.94	1.04	1.26
Bos javanicus	2	750.00	450.00	5.42	3.90	1.03	1.20
Bos taurus	1	384.00	327.50	3.22	2.90	1.01	1.05
Boselaphus tragocamelus	2	253.33	136.33	2.34	1.55	1.03	1.23
Bubalus bubalis	1	1200.00	800.00	7.83	6.04	1.03	1.16
Bubalus depressicornis	1	156.00	145.00	1.61	1.53	1.00	1.02
Budorcas taxicolor	2	282.67	160.00	2.54	1.74	1.03	1.21
Camelus dromedarius	2	545.00	545.00	4.23	4.23	1.00	1.00
Capra aegagrus	2	52.97	38.59	0.70	0.56	1.00	1.10
Capra caucasica	2	86.25	55.00	1.02	0.75	1.01	1.15
Capra cylindricornis	2	82.83	50.00	0.99	0.70	1.01	1.17
Capra falconeri	2	92.66	36.25	1.08	0.57	1.03	1.36
Capra ibex	2	80.50	48.90	0.97	0.69	1.01	1.17
Capra pyrenaica	2	72.50	40.00	0.89	0.59	1.01	1.20
Capreolus capreolus	1	24.16	23.36	0.39	0.38	1.00	1.01
Capricornis sumatraensis	2	95.33	93.75	1.10	1.09	1.00	1.01
Cephalophus callipygus	0	18.63	18.41	0.32	0.31	1.00	1.00
Cephalophus dorsalis	0	20.25	19.51	0.34	0.33	1.00	1.01
Cephalophus jentinki	0	70.31	80.51	0.87	0.96	1.00	0.96
Cephalophus leucogaster	0	16.07	17.85	0.28	0.30	1.00	0.97
Cephalophus maxwelli	0	6.50	7.20	0.14	0.15	1.00	0.97
Cephalophus monticola	0	4.38	5.11	0.11	0.12	1.00	0.96
Cephalophus natalensis	0	13.05	12.09	0.24	0.23	1.00	1.02
Cephalophus niger	0	19.85	18.38	0.33	0.31	1.00	1.02
Cephalophus nigrifrons	0	13.34	15.03	0.24	0.27	1.00	0.97
Cephalophus ogilbyi	0	20.41	22.50	0.34	0.36	1.00	0.97
Cephalophus rufilatus	0	10.10	10.30	0.20	0.20	1.00	0.99
Cephalophus spadix	0	55.55	61.19	0.73	0.78	1.00	0.97
Cephalophus sylvicultor	0	52.50	71.95	0.70	0.87	1.00	0.91
Cephalophus zebra	0	13.85	14.70	0.25	0.26	1.00	0.98
Cervus axis	2	80.74	48.67	0.97	0.68	1.01	1.17
Cervus canadensis	2	335.00	252.00	2.90	2.40	1.01	1.10
Cervus duvauceli	2	223.06	142.02	2.12	1.56	1.02	1.16
Cervus elaphus	2	185.09	140.16	1.83	1.52	1.01	1.09
Cervus eldi	2	105.00	72.00	1.19	0.92	1.01	1.13
Cervus nippon	2	56.45	37.40	0.74	0.55	1.01	1.13
Cervus timorensis	2	73.00	53.00	0.90	0.72	1.01	1.10
Cervus unicolor	2	206.26	131.80	1.99	1.47	1.02	1.16
Connochaetes gnou	1	166.67	135.00	1.69	1.46	1.01	1.07
Connochaetes taurinus	1	235.28	184.91	2.21	1.87	1.01	1.08
Dama dama	2	68.05	44.58	0.85	0.63	1.01	1.14
Damaliscus dorcas	2	71.10	69.22	0.88	0.86	1.00	1.01
Damaliscus hunteri	1	91.00	86.00	1.06	1.02	1.00	1.02
Damaliscus lunatus	1	137.00	120.15	1.45	1.33	1.00	1.04
Dorcatragus megalotis	0	9.98	10.66	0.20	0.21	1.00	0.98
Elaphodus cephalophus	0	18.00	18.00	0.31	0.31	1.00	1.00
Elaphurus davidianus	2	207.25	149.85	2.00	1.61	1.01	1.11
Gazella cuvieri	0	29.38	20.38	0.45	0.35	1.00	1.11
Gazella dama	0	68.00	51.00	0.85	0.70	1.00	1.09

(continued)

Table 2. (*continued*)

Species	Sexual segregation	Body mass (kg)		Maintenance requirement (kg dry mass/day)		Activity ratio, α (Female:Male)	
		Male	Female	Male	Female	Feeding rate ∝ $BM^{0.71}$	Feeding rate ∝ $BM^{1.0}$
Gazella dorcas	0	16.28	13.30	0.28	0.25	1.00	1.06
Gazella gazella	0	23.34	20.75	0.37	0.34	1.00	1.03
Gazella granti	0	72.09	45.95	0.89	0.65	1.01	1.15
Gazella leptoceros	0	27.21	20.88	0.42	0.35	1.00	1.08
Gazella rufifrons	0	27.00	20.67	0.42	0.35	1.00	1.08
Gazella soemmerringi	0	45.35	33.57	0.62	0.50	1.00	1.09
Gazella spekei	0	21.32	16.64	0.35	0.29	1.00	1.07
Gazella subgutturosa	0	27.35	22.97	0.42	0.37	1.00	1.05
Gazella thomsoni	0	22.72	17.75	0.37	0.31	1.00	1.07
Giraffa camelopardalis	2	1190.23	814.34	7.78	6.10	1.03	1.15
Hemitragus hylocrius	2	100.00	50.00	1.14	0.71	1.02	1.25
Hemitragus jayakari	1	26.50	17.00	0.41	0.30	1.00	1.14
Hemitragus jemlahicus	1	103.25	56.00	1.17	0.77	1.02	1.22
Hippocamelus bisulcus	0	65.00	55.00	0.82	0.73	1.00	1.05
Hippotragus equinus	2	274.40	256.40	2.49	2.37	1.00	1.02
Hippotragus niger	2	235.24	216.63	2.21	2.09	1.00	1.03
Hydropotes inermis	0	12.23	13.27	0.23	0.24	1.00	0.98
Hyemoschus aquaticus	0	9.84	12.02	0.19	0.22	1.00	0.95
Kobus ellipsiprymnus	2	236.75	187.31	2.22	1.89	1.01	1.08
Kobus kob	2	97.46	61.86	1.12	0.82	1.01	1.15
Kobus leche	2	104.32	78.69	1.18	0.97	1.01	1.09
Kobus vardoni	2	76.04	63.48	0.93	0.82	1.00	1.06
Lama guanicoe	0	109.50	99.00	1.22	1.14	1.00	1.03
Litocranius walleri	2	34.97	34.33	0.51	0.50	1.00	1.01
Madoqua guentheri	0	3.73	4.50	0.09	0.11	1.00	0.95
Madoqua kirki	0	4.60	5.11	0.11	0.12	1.00	0.97
Madoqua saltiana	0	2.27	2.64	0.06	0.07	1.00	0.96
Mazama americana	0	32.50	29.13	0.48	0.45	1.00	1.03
Mazama gouazoubira	0	7.88	20.63	0.16	0.33	1.02	0.77
Moschus moschiferus	0	13.00	14.67	0.24	0.26	1.00	0.97
Muntiacus crinifrons	0	23.10	24.10	0.37	0.38	1.00	0.99
Muntiacus muntjak	0	20.93	15.09	0.35	0.27	1.00	1.10
Muntiacus reevesi	0	14.68	11.77	0.26	0.22	1.00	1.07
Nemorhaedus goral	1	32.00	29.95	0.48	0.46	1.00	1.02
Neotragus batesi	0	2.42	2.78	0.07	0.07	1.00	0.96
Neotragus moschatus	0	4.78	5.06	0.11	0.12	1.00	0.98
Neotragus pygmaeus	0	2.00	2.20	0.06	0.06	1.00	0.97
Odocoileus hemionus	2	70.32	46.86	0.87	0.66	1.01	1.13
Odocoileus virginianus	2	57.58	47.10	0.75	0.65	1.00	1.06
Okapia johnstoni	0	200.00	200.00	1.95	1.95	1.00	1.00
Oreamnos americanus	2	95.89	61.00	1.11	0.81	1.01	1.15
Oreotragus oreotragus	1	11.29	12.95	0.22	0.24	1.00	0.96
Oryx gazella	1	178.03	166.43	1.78	1.70	1.00	1.02
Oryx leucoryx	2	85.90	80.10	1.02	0.97	1.00	1.02
Ourebia ourebi	0	14.12	15.10	0.26	0.27	1.00	0.98
Ovibos moschatus	1	356.00	247.33	3.04	2.38	1.02	1.13
Ovis ammon	1	120.73	63.20	1.32	0.85	1.02	1.23
Ovis canadensis	2	83.37	58.73	0.99	0.78	1.01	1.11
Ovis dalli	2	80.45	53.31	0.97	0.73	1.01	1.14
Ovis nivicola	2	103.05	53.04	1.17	0.74	1.02	1.24
Ovis orientalis	2	67.88	44.90	0.85	0.64	1.01	1.14
Pantholops hodgsoni	2	42.33	25.80	0.59	0.42	1.01	1.16
Pelea capreolus	1	24.00	25.02	0.38	0.39	1.00	0.99
Procapra gutturosa	0	31.54	24.01	0.47	0.39	1.00	1.08
Pseudois nayaur	2	60.00	39.50	0.77	0.58	1.01	1.14
Pudu mephistophiles	0	13.16	13.84	0.24	0.25	1.00	0.99
Pudu pudu	0	10.13	10.85	0.20	0.21	1.00	0.98
Rangifer tarandus	2	145.00	85.82	1.52	1.06	1.02	1.18
Raphiceros campestris	1	10.87	11.29	0.21	0.22	1.00	0.99
Raphiceros melanotis	1	10.72	10.46	0.21	0.20	1.00	1.01
Raphiceros sharpei	1	7.35	7.77	0.16	0.16	1.00	0.98
Redunca arundinum	1	58.26	43.19	0.75	0.61	1.00	1.10
Redunca fulvorufula	1	30.10	28.51	0.46	0.44	1.00	1.02
Redunca redunca	1	51.55	40.25	0.69	0.58	1.00	1.08
Rupicapra rupicapra	2	40.33	31.67	0.57	0.48	1.00	1.07

Table 2. (continued)

Species	Sexual segregation	Body mass (kg)		Maintenance requirement (kg dry mass/day)		Activity ratio, α (Female:Male)	
		Male	Female	Male	Female	Feeding rate $\propto BM^{0.71}$	Feeding rate $\propto BM^{1.0}$
Saiga tatarica	2	42.50	32.33	0.59	0.49	1.00	1.09
Sylvicapra grimmia	0	18.33	19.64	0.31	0.33	1.00	0.98
Syncerus caffer	1	642.94	467.50	4.81	3.90	1.02	1.12
Tetracerus quadricornis	0	18.00	17.00	0.31	0.30	1.00	1.02
Tragelaphus angasi	2	110.16	64.40	1.23	0.85	1.01	1.19
Tragelaphus buxtoni	2	232.00	166.67	2.18	1.75	1.01	1.11
Tragelaphus imberbis	2	95.63	62.13	1.10	0.82	1.01	1.14
Tragelaphus oryx	2	647.33	415.75	4.84	3.62	1.03	1.17
Tragelaphus scriptus	2	49.68	31.09	0.67	0.48	1.01	1.15
Tragelaphus spekei	2	102.33	60.19	1.16	0.81	1.01	1.18
Tragulus javanicus	0	240.82	159.25	2.25	1.70	1.02	1.14
Tragulus meminna	0	1.30	1.46	0.04	0.05	1.00	0.97
Tragulus napu	0	3.06	4.64	0.08	0.11	1.01	0.89
Vicugna vicugna	0	5.80	5.90	0.13	0.13	1.00	1.00

Species are classified into one of three segregation classes: 0 = species that show no segregation; 1 = species that are territorial or show temporary segregation; 2 = species that show sexual segregation. BM: body mass. Sources are given in Pérez-Barbería & Gordon 2000.

observed in field conditions is valid because the predicted value of segregation would be almost unnoticeable under field conditions.

FORCING INTERGROUP SYNCHRONICITY

Activity synchronization is an important factor in explaining sexual segregation in mammals (Conradt 1998a; Conradt & Roper 2000, 2003). Field studies of the costs of activity synchronization are still lacking, but Conradt & Roper (2000) estimated that for red deer, sex differences in activity synchrony could explain approximately one-third of the observed sexual segregation. Conradt (1998a) suggested that activity patterns are more difficult to

Figure 3. The relation between sexual body mass dimorphism and activity ratio for the species in Table 2. The calculation of the activity ratio is described in the Appendix. Circles and diamonds assume that feeding rate scales with body mass to the power of 0.71 (Shipley et al. 1994) and 1.0, respectively.

synchronize in mixed-sex groups, and as a consequence single-sex groups would emerge, so that activities can be easily synchronized. We have included a forced synchronicity into our simulations, assuming that all animals become active (or inactive) at a set time each day, and that an animal's state does not change until its daily maintenance requirement has been met. This assumption mimics the observation that most animal species have circadian cycles of activity, although there can be many other events that cause synchronicity (e.g. weather, disturbance). The results of the simulations indicate that forced synchronicity accentuates the effect of activity budget differences, especially where differences are small, although the increase in segregation was never great (Fig. 4).

The incorporation of a forced activity synchronization has two effects on sexual segregation. It reduces sexual segregation during the period when both sexes are in the same activity state, but it can also increase sexual segregation because the difference in maintenance requirements between males and females means that there is a period when one sex will be active and the other inactive. In our model, the overriding effect of synchronization is to increase sexual segregation. For other animal movement behaviours it is possible that activity synchronization will reduce sexual segregation. For example, if males and females use the same resting areas, then a forced synchronization (e.g. at sunrise or sunset) will quickly remove any sexual segregation that has developed since the last forced synchronization (Corti & Shackleton 2002). In this scenario the values of segregation will oscillate, giving a small long-term average.
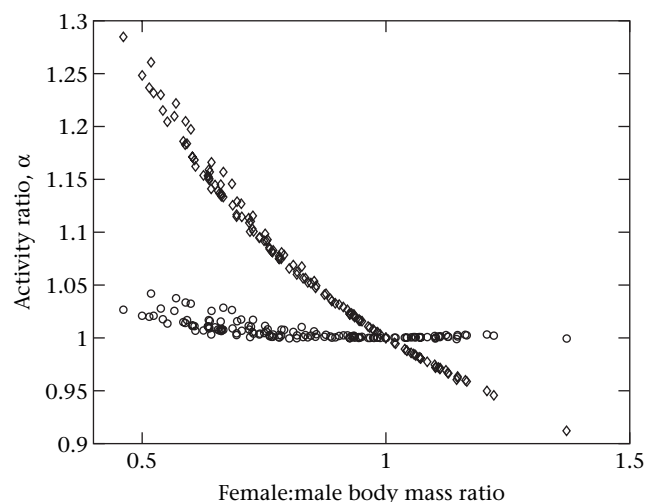
THE MOVEMENT RULE AND TRANSIENT EFFECTS

In the original model an animal moves towards the nearest moving animal, provided the separation is not greater than d. This movement rule directly implies that if one sex moves more frequently than the other then this
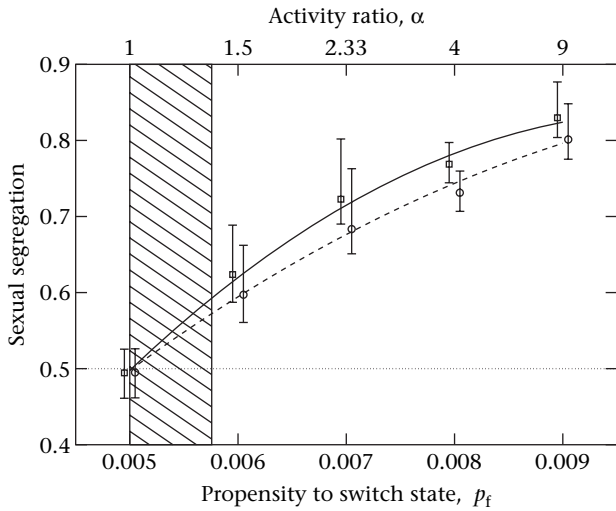
Figure 4. Model predictions of sexual segregation assuming activity is synchronized at the start of each day. Solid and dashed lines are the best-fit quadratic regression lines for females and males, respectively. Error bars show the range of data from 10 runs of the model, the mean value is indicated by the marker, and the hatched region and horizontal dotted line are the same as in Fig. 2. For clarity the values along the X axis for males and females have been slightly displaced.

sex will tend to be more clustered. We investigated the robustness of the model by changing this movement rule so that an animal will move towards its nearest neighbour regardless of the activity state and sex of the neighbour. As a result the segregation was greatly weakened (Fig. 5a) suggesting that the model is sensitive to the movement rule. This weakening of sexual segregation was found for all values of d. These two movement rules are two contrasting possibilities amongst a range of possibilities, but how realistic are any of these rules? Field observations indicate that conspecific copying behaviour affects social aggregation (Wagner & Danchin 2003), and modelling work suggests that it can incur a significant energy cost for the group (Conradt & Roper 2000, 2003). For example, despotic decisions (i.e. one animal conditioning the behaviour of the whole group) could reinforce segregation because it increases group aggregation, but this would not match with the assumption of the activity budget hypothesis, because the behaviour of the group would be ruled by social factors rather than differences in body mass. What seems likely is that the movement rule is the product of both the activity budget and leadership decisions, and the outcome is likely to weaken segregation, as our simulation demonstrates.

With our new movement rule, significant sexual segregation appears only for extreme activity ratios ($\alpha > 4$). The presence of any sexual segregation may seem somewhat surprising, because in the long term the two sexes would be expected to diffuse evenly throughout their home range, producing no sexual segregation. The reason that sexual segregation is seen at all in Fig. 5a is because our results include the transient dynamics rather than the long-term dynamics. This is illustrated in Fig. 5b for the mean time course of 10 simulations with $p_f = 0.008$.
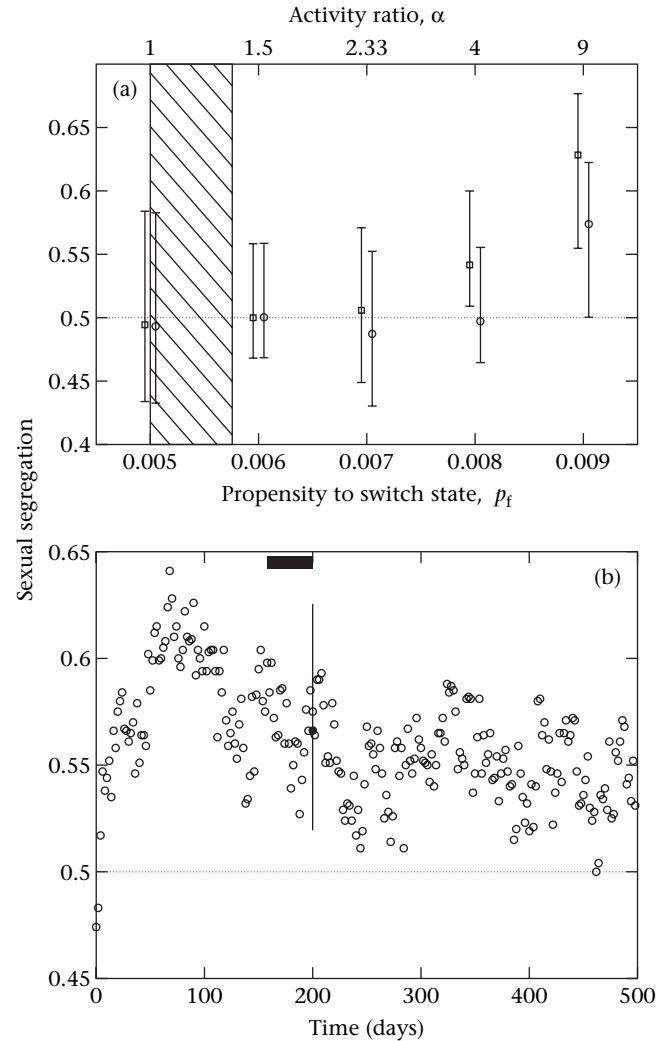

Figure 5. (a) The effect of changing the movement rule upon the predicted degree of sexual segregation for all animals. Animals move towards their nearest neighbour, regardless of its activity. The initial distribution of animals is random within a 0.1×0.1 square centred in the middle of the model's arena. Segregation is predicted only at extreme differences in activity (activity ratio ca. 9). Hatched region and horizontal dotted line are the same as in Fig. 2. (b) The mean sexual segregation over 10 simulations for both sexes when $p_f = 0.008$ as a function of time. The reason for the sexual segregation seen in (a) at high activity differences can be seen as a transient effect: females 'diffuse' through the environment faster than males, initially generating sexual segregation which slowly decays. The error bar shows the range of sexual segregation for the 10 simulations after 200 days (the usual end point of a simulation) averaged over the last 1000 iterations (shown by the solid bar).

Initially, animals are randomly positioned in a localized area, so at $t = 0$ there is no segregation. Segregation is generated as the more active animals (females) move into the surrounding space at a faster rate than the less active animals (males). This spatial distribution with its sexual segregation is a transient feature. Segregation reaches a maximum after 100 days because males also move out and fill the model arena, causing a gradual decline in the sexual segregation as the long-term equilibrium is

approached. Increasing the size of the arena would increase both the strength and the time taken to reach the maximum segregation. In the unrealistic limit of an infinite arena, sexual segregation would continually increase.

DISCUSSION

Assumptions of the Activity Budget Hypothesis

The activity budget model of Ruckstuhl & Kokko (2002) contains two important assumptions: (1) animals have a tendency to move towards the closest moving animal regardless of their sex, and (2) the activity budgets of animal cohorts differ significantly, which in turn requires a strong dimorphism in body mass. Under these assumptions the model is able to explain (1) sexual segregation, when there is sexual dimorphism in body size or (2) social segregation, if the dimorphism in body size occurs between animals of different cohorts or phenotypes. This makes the model attractive, because it has the potential to explain segregation across a variety of conditions and organisms (Michelena et al. 2004). It is therefore disappointing to find that when the model is parameterized using real data or when the movement rule of the model is changed, the predicted level of segregation is relatively small.

The activity budget hypothesis has two key assumptions: females digest forage less efficiently than males, and large differences in activity budgets make synchrony of behaviour difficult (Ruckstuhl & Neuhaus 2002, see Introduction). These assumptions differ from those of the activity budget model. The second assumption was studied by Conradt & Roper (2000), who modelled activity synchronization and found that it could explain a third of the observed sexual segregation in red deer. The activity budget model does not include a cost of asynchrony, but does consider differences in activity caused by differences in body mass. We suggest that the only prerequisite for the activity budget hypothesis to work is a large difference in body mass, between either sexes or cohorts. Our results show that an activity ratio of $\alpha > 2$ is required to generate significant levels of sexual segregation from the model (Figs 2, 4). In terms of activity budgets this translates into one sex or cohort being at least twice as active as another. Based upon allometric scaling rules (Fig. 3), this would require a much larger body size dimorphism than those observed in segregating ungulates (Shipley et al. 1994).

Differences in activity, caused by the allometry of energy requirements, may be accentuated by sexual differences in the efficiency of fibre digestion. The less efficient sex at digesting fibre should select more highly digestible foods for its diet, which presumably requires more searching time and consequently more time being active. However, there is no evidence for sexual differences in the efficiency of fibre digestion other than those related to body size. Females are thought to be less efficient than males at digesting fibre because females are generally smaller than males, but this assumption is based on scaling studies from a range of species whose body masses span three orders of magnitude (Robbins 1993). For ungulates, the sexual difference in the digestion efficiency of fibre should be very small, since the average male to female body mass ratio is only 1.5 in segregating species, with a maximum of 2.6 (Pérez-Barbería & Gordon 2000). This implies that sexual differences in fibre digestion will contribute little to sexual differences in activity budgets, and suggests that this issue needs further investigation.

Including activity synchronization in the model promotes sexual segregation (Fig. 4), but estimated activity ratios are still too small to generate significant segregation. Sexual segregation is weakened still further if the movement rule is changed. A movement rule that treats all animals equally produces almost no segregation (Fig. 5a). Some segregation is predicted at high activity ratios, and this is due to the transient spatial distribution of the animals brought about by changes in their home range over time. Transient effects are increasingly being recognized as an important feature of ecological systems (Hastings, 2004) because timescales are frequently too short for equilibrium behaviour to dominate. Transient effects may be an important link between activity budgets and segregation because this mechanism of generating segregation is largely independent of an animal's movement rule. Transient spatial distributions will show segregation provided that: (1) there is a difference in activity budgets between cohorts; (2) a population's home range changes in size periodically; and (3) changes in home range size persist long enough to allow the separation of active cohorts from less active cohorts (Fig. 5b).

The sensitivity of the model to the movement rule suggests that social factors (defined as behavioural or physiological factors that generate an affinity for specific peers of either sex, which are not explained by differences in body size) could play a decisive role in the model, because the movement rule defines how an individual moves relative to other members of the group. It is important to be clear that the activity budget hypothesis proposes that activity differences underlie animal aggregation/segregation, whereas the social factors hypothesis proposes that social factors underlie animal aggregation/ segregation. A combination of these two factors might occur, but the two hypotheses should not be confused. The importance of the social factors hypothesis must not be underestimated. This is clearly seen in Figs 1, 2; the activity budget model, as it stands, cannot generate a pattern of segregation in which each sex aggregates into a few groups (by classifying individuals into groups, predicted group size could also be compared against data). This is obviously because the model does not take into account a social rule in which increasing group size increases the aggregation of new members and also stabilizes the aggregations already formed. In the model, activity differences alone explain a limited amount of segregation and social rules are needed to achieve the levels of intrasex aggregation observed in ungulate populations in the field. To explain sexual segregation, all of the hypotheses proposed in the literature require the existence of social bonds to some extent. If there were no social bonds between animals then individuals would simply disperse without forming the compact and stable groups observed in field conditions.

Evidence for the Activity Budget Hypothesis

A comprehensive literature review (Ruckstuhl & Neuhaus 2002) resulted in overwhelming support for the activity budget hypothesis compared with the predation risk and forage selection hypotheses. It is arguable whether the rationale used in the study of Ruckstuhl & Neuhaus was appropriate for carrying out an unbiased comparison of these three hypotheses. For example, Ruckstuhl & Neuhaus detailed behavioural data in four species, and in two of these species the first prediction of the activity budget hypothesis was supported (i.e. females graze longer than males while males spend more time ruminating or lying, Table 1 in Ruckstuhl & Neuhaus 2002). In these four species data were available on time spent feeding and diet selection. The extension of this test to the other species in the review, however, is confounded by the fact that there are no data on diet selection (food availability is unknown), because differences in diet selection between males and females can account for differences in grazing time. Rather than directly testing the first prediction of the activity budget hypothesis, Ruckstuhl & Neuhaus inferred it by testing whether sexual differences in the time spent feeding would be greater for species of 'intermediate feeders' than 'bulk feeders', but no difference was found. A meta-analysis that attempts to test rigorously the first prediction of the activity budget hypothesis will require reliable information on: (1) the quantity, quality and distribution of available forage; (2) habitat use; and (3) the diet consumed by the species studied, because the time that an animal spends foraging depends on these factors (Spalinger & Hobbs 1992; Gross et al. 1993; Owens et al. 1995).

The activity budget hypothesis has also been questioned by recent field studies, which suggest that other factors can override its predictions. Michelena et al. (2004) tested the activity budget hypothesis using 15 male and 15 female adult merino sheep, *Ovis aries*, in 1-ha paddocks during a 7-week period in winter. Although this experiment did not reproduce conditions in the wild (i.e. food, habitat fragmentation, scale), it is appropriate for validating those predictions of the activity budget hypothesis that are independent of the species used (domestic or wild), the habitat scale, and the quality and distribution of the food. Michelena et al. (2004) found that despite a high average sexual dimorphism in body mass (female to male body mass ratio of 2/3) there was no perceptible sexual segregation and a high synchronization between the activities of males and females. The differences in body mass in their study give an activity ratio of $\alpha = 1.1$, which from our Fig. 2 would not be sufficient to produce detectable segregation based upon the model of Ruckstuhl & Kokko (2002). Another recent study has tested the activity budget hypothesis for *O. canadensis* in field conditions (Mooring et al. 2003). Contrary to the activity budget hypothesis, these authors found no differences between the sexes in the time spent foraging, moving, resting or ruminating (for a discussion see Mooring & Rominger 2004; Neuhaus & Ruckstuhl 2004a,b).

Conclusions

Earlier work has shown that the activity budget hypothesis is likely to play a role in explaining the observed sexual segregation. Conradt & Roper (2000) looked at sexual differences in activity synchrony for red deer, and concluded that it could explain only one-third of the observed sexual segregation. Our work is the first time that the size of the activity budget effect resulting from a sexual dimorphism in body mass has been quantitatively compared with data. Comparing our simulations against the observed range of body mass dimorphism in ungulates shows that activity budgets (estimated from maintenance requirements) alone are insufficient to explain the high degree of sexual segregation observed in the field. However, the simulations do suggest two factors that may accentuate the effect of activity budget differences. First, activity synchronization can increase sexual segregation, although the increases found in our simulations were not sufficient to change our general conclusions. Second, the transient spatial distribution of a population, following seasonal changes in the home range area, generates sexual segregation if males and females differ in activity budgets. While our estimates of this effect for red deer in the Grampian region of Scotland suggest that transient sexual segregation is unlikely to be significant for this species, the effect may be more significant for other species.

Our failure to understand sexual segregation may be caused by our insistence in pursuing a physiological explanation. We suggest that a more fruitful approach would be to understand sexual differences in behaviour and use them to unravel the complex factors involved in sexual segregation.

Appendix: Parameterization Details

The model was parameterized so that the size of the model's arena and the speed of an animal's movement corresponded to GPS data of red deer stags in the Grampian region of Scotland (Sibbald et al. 2001). Equivalent data for females were unavailable, so their speed and home range were assumed to be the same as a male's. The assumption of no difference between the home range areas of males and females is supported by the results of Mysterud et al. (2001). The speed of a red deer stag was taken to be 5 km/day (this can range from 3 km/day in the winter to more than 6 km/day during the summer, Sibbald et al. 2001). The annual home range was taken to be approximately 200 km^2 (A. M. Sibbald & R. J. Hooper, personal communication) making the physical extent of the model arena 14×14 km. We let a model animal update its behavioural state every hour, making the step size of the model 0.21 km (normalizing, so that the model gives a step size, $s = 0.21/14 = 0.015$). Animals were assumed not to conform to the behaviour of their

neighbours ($c = 0$), and the maximum nearest-neighbour distance was taken to be the extent of the model ($d = 1$), because Ruckstuhl & Kokko found that the values of c and d had no significant effect upon sexual segregation. All other parameters and model formulation were the same as those used by Ruckstuhl & Kokko (Table 1). Each run lasted 200 days with 24 steps/day, making 4800 iterations of which the last 1000 were used for the final results. Each parameterization was repeated 10 times with random initial positions for each animal.

The relative activities of the two sexes for a range of large ungulate species were calculated from data on the body weights of males and females and by assuming forage of average hay. The maintenance requirement (MR) was calculated using the formula $\mathrm{MR} = D(F + A)/(k_m\mathrm{MEA})$ (kg DM/day), where $F = 0.23 \ (\mathrm{BM}/1.08)^{0.75}$ (MJ/day) is the fasting metabolism, MEA = 8.3 (MJ/kg DM) is the metabolizable energy of a medium-quality hay, $D = 0.850$ is the dry matter content of hay, $k_m = 0.35q_m + 0.503$ is the efficiency of utilization of metabolizable energy for maintenance, $q_m = 0.46$ is the digestibility of hay, $A = 0.0054$ BM (MJ/day) is the activity allowance estimated from housed pregnant ewes (AFRC 1993) and BM is the body mass (kg). Hay is a good average food type for the wide range of foods used by ungulates in Table 2. The relative activity of the two sexes is quantified using the activity ratio, α, which is the ratio of female to male maintenance requirements scaled relative to feeding rate, giving a measure of the time spent feeding by a female compared to that of a male (Fig. 3). At its simplest, feeding rate will be equivalent to an animal's food intake rate, but other behavioural factors may affect feeding rate. Shipley et al. (1994) found that intake rate scaled to $\mathrm{BM}^{0.71}$ in 12 species of herbivorous mammal. However, feeding may incorporate more behavioural factors than just food intake, and these additional factors may mean that feeding rate scales with an allometric exponent closer to unity. Figure 3 shows the relation between body mass dimorphism and activity ratio for these feeding rate allometries of $\mathrm{BM}^{0.71}$ and $\mathrm{BM}^{1.0}$. Since a feeding rate proportional to body mass gives a greater range of activity ratios (Fig. 3), and is more consistent with the data compiled by Ruckstuhl & Neuhaus (2002), we used this allometric scaling for feeding rate. This makes the activity ratio $\alpha = (\mathrm{MR}_\female/\mathrm{MR}_\male)(\mathrm{BM}_\male/\mathrm{BM}_\female)$.

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