



## Causes of natal dispersal in a monogamous ungulate, the Japanese serow, *Capricornis crispus*

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We examined two hypotheses to explain the natal dispersal of Japanese serows: competition for mates and/or resources and inbreeding avoidance. We predicted that if the competition hypothesis were valid, serow offspring would disperse when the same-sex but not opposite-sex parent was present, whereas if the inbreeding avoidance hypothesis were valid, the opposite would apply. Only adult males were aggressive, and only to male offspring; this aggression may have led to offspring dispersing, although, over the 29-year study, no significant sex difference was found in the dispersal rate, mean age at dispersal or dispersal distance. All philopatric offspring, one male and two females, remained in the natal home ranges after the disappearance of the same-sex parent or territorial resident, and all 30 dispersals of both sexes occurred when the same-sex parent or territorial resident was present in the natal home ranges. Four male and five female offspring, however, left the natal home ranges after their opposite-sex parent had already disappeared. These results suggest that serow dispersal can be explained by the competition hypothesis.

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Natal dispersal is defined as the movement of an individual from its birth site to its first breeding or potential breeding site (Howard 1960; Greenwood 1980). The pattern, functions, causes and consequences of natal dispersal have attracted considerable attention from biologists. Three major causes of natal dispersal have been suggested: (1) competition for mates (Dobson 1982; Moore & Ali 1984; Liberg & von Schantz 1985); (2) competition for environmental resources (Waser 1985; Favre et al. 1997); and (3) avoidance of inbreeding (Packer 1979; Cockburn et al. 1985; Pusey 1987; Clutton-Brock 1989; Wolff 1992; Sweitzer & Berger 1998). Although each hypothesis has its supporters (see Moore & Ali 1984; Packer 1985), several recent studies have suggested that the causes of dispersal are complex: McNutt's (1996) and Loew's (1999) studies supported both the mate competition and inbreeding avoidance hypotheses, whereas

Gundersen & Andreassen (1998) found evidence for the resource competition and inbreeding avoidance hypotheses. The three hypotheses can be reclassified into two: the competition hypothesis and the inbreeding avoidance hypothesis. Intrasexual relationships between resident adults and offspring in the natal home ranges would be noteworthy in the competition hypothesis, because competition for mates or resources tends to be more critical between individuals of the same sex than between opposite sexes, whereas intersexual relationships between offspring and their close relatives would be important in the inbreeding avoidance hypothesis. Wolff (1993) suggested that if the competition hypothesis were valid, natal dispersal would be correlated with the presence of the same-sex but not opposite-sex parent, whereas if the inbreeding avoidance hypothesis were valid, the opposite would apply.

The Japanese serow is a good test species for Wolff's prediction, because it is a solitary, monogamous ungulate and each offspring has only two adults in its natal home range: an adult female, usually the mother, and an adult male, the mate of the mother and the probable father. Swilling & Wooten (2002) have suggested that study of a monogamous system is valuable for investigating animal

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dispersal, because it allows a greatly simplified interpretation of dispersal data.

Japanese serows inhabit mountain forests of Japan. They show little sexual dimorphism; both sexes weigh 30–45 kg, and have horns 12–16 cm long. Adults of both sexes maintain intrasexually exclusive territories and usually live alone. Monogamous pair bonds maintained over several years are evident in the range overlap between a male and one female (or sometimes two or three; Ochiai 1983a,b; Kishimoto 1989; Kishimoto & Kawamichi 1996; Ochiai & Susaki 2002). Single kids are usually born in May–June. The mean fertility or reproductive rate of adult females in two free-living populations was 72% (Miura et al. 1987) and 81% (Kishimoto 1989). Yearlings begin to become independent, but still remain within the mothers' territories. When offspring approach sexual maturity, they leave the natal home ranges to establish their own territories elsewhere (Ochiai 1983a; Kishimoto 1987, 1989). In radiotelemetry study of four juvenile Japanese serows, the longest dispersal distance was 4 km for a male (Okumura et al. 1996).

Although it is difficult to observe solitary ungulates inhabiting forests, and interactions between individuals are rare, we have carried out a long-term study to analyse Japanese serow dispersal. Our aim was to examine the dispersal process and characteristics such as dispersal rate, age and distance and any sex differences. Our specific objective was to test Wolff's prediction. We predicted that if the competition hypothesis were valid, then serow offspring would disperse when the same- but not opposite-sex parent or adult was present. Conversely, if the inbreeding avoidance hypothesis were valid, then offspring would disperse when the opposite- but not same-sex parent was present.

## METHODS

### Study Area

The study area (100 ha) is situated in Wakinosawa (41°9'N, 140°49'E), Mutsu City, on the Shimokita Peninsula, Aomori Prefecture, northern Japan. The area faces Mutsu Bay on its southern and western sides. It ranges in elevation between 0 and 240 m, and the slopes are steep (around 25°). The area is part of the larger serow habitat in the northern part (1100 km<sup>2</sup>) of the Shimokita Peninsula. The climate belongs to the cool temperate zone; mean annual temperature is 9.3°C, mean monthly temperatures range from –1.8°C in February to 21.5°C in August, and mean annual precipitation is 1337 mm at the nearest meteorological station, 4 km east of the study area. The area is covered by 10–100 cm of snow in winter, and snow cover persists for 3 months between late December and March. The vegetation consists principally of mature deciduous broadleaved forest (75% of the area) dominated by Mongolian oak, *Quercus mongolica*, and Japanese beech, *Fagus crenata*. Conifer plantations (Japanese cedar, *Cryptomeria japonica*, and Japanese red pine, *Pinus densiflora*) and natural coniferous forest of hiba arborvitae, *Thuja dolabrata* var. *hondae*, cover 13% and 7% of the

area, respectively. Since the extinction of the wolf, *Canis lupus*, from Japan in the early 1900s, Japanese serows have generally had no predators and serows inhabiting the study area are not at risk of predation. Hunting of serows has been prohibited for several decades in Aomori Prefecture. The Japanese serow is the only species of ungulate inhabiting the study area, and has maintained a stable population density with a mean  $\pm$  SD of  $14.2 \pm 2.5$  individuals/km<sup>2</sup> from 1976 to 2000 (Ochiai & Susaki 2002). The mean population density of Japanese serows in 174 census areas of 10 prefectures was 2.6 individuals/km<sup>2</sup> (Maruyama & Furubayashi 1980), so the density of serows in the study area was high and the habitat was almost completely saturated with adult serow territories.

### Field Observation

We conducted field observations on 1132 days from 1976 to 2005. The mean  $\pm$  SD number of annual field observations was  $39.0 \pm 24.7$  days ( $N = 29$  years). Serows were observed directly for 2475 h. We walked through the study area searching for serows, and then observed their behaviour through binoculars (7 $\times$ , 8 $\times$ ) and a telescope (25 $\times$ ). Their tracking routes were recorded on a 1:5000-scale map. Serows inhabiting the study area were relatively tame in the presence of humans and we were able to observe their natural behaviour at a distance of 10–30 m. The duration of one observation varied considerably, ranging from momentary sightings to 8 h or more. We investigated social interrelations of serows via direct observations of interactions and behaviour of identified individuals. We identified all 101 individuals in the study area by their natural features, including the shape of their horns, scars on the face or ear, and facial markings. A major clue to individual identification was the shape of the horns, particularly asymmetry in length and curving between a pair of horns. The identities of the mothers were of particular help in identifying the kids. Sex was determined from visible external genitalia. Animals were classified by age as kid (<12 months old), yearling (12–23 months old), 2 years (24–35 months old) and  $\geq 3$  years on the basis of horn development and continuous observations from infancy. Because both male and female serows become sexually mature between 2 and 3 years of age (Sugimura et al. 1981; Tiba et al. 1988), 'adult' refers to individuals  $\geq 3$  years old. 'Offspring' refers to serows that were born and grew up in the study area, regardless of age. During observations, we noted any aggressive interactions between adults and offspring. Aggressive behaviour comprised mild and severe chasing, butting and mutual butting; a serow would allow its opponent to be near during mild chasing, but not during severe chasing. Sexual behaviour comprised genital sniffing, flehmen, foreleg kicking, pushing with the forehead and the base of the horns, chasing and mounting.

### Data Analyses

The frequency of association between two serows was calculated as  $A/B$  where  $A$  equals the number of observation

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