Strategy of female tigers to avoid infanticide

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In felids, mortality caused by dominant males can affect life history characteristics, demography and reproductive success. When a dominant male is removed, an incoming male may kill offspring sired by the previous male to induce the resident female into oestrus. We had the opportunity to observe the infanticide avoidance responses of female tigers (Panthera tigris) to incoming males in the core area of Ranthambhore Tiger Reserve (RTR), Rajasthan, during 2008-2010. In one case, following the disappearance of a dominant male tiger (TM-12) from the established territory of a female tiger (TF-13), the female tiger, accompanied by two cubs, immediately moved approximately 20 km away into riverine areas outside the protected area of RTR. In another case, a female (TF-04) died from a battle with a male while defending her cubs. These observations reveal the attempts of female tigers to avoid infanticide. Observations and results from behavioural decisions made by tigers are important to understand the species and the factors that facilitate their conservation.

Keywords: Camera trap, female tigers, infanticide avoidance, Ranthambore Tiger Reserve.

IN carnivores, adult males play an important role in population dynamics, reproduction and breeding success^{1,2}. Removal of adult territorial males can led to increased immigration of new males, reduced survival of cubs and reduced population growth³⁻⁷. Infanticide by immigrating males is a male reproductive strategy whereby new males may kill the offspring sired by the dominant male to enable the mother to come into oestrus earlier (i.e. killing for accelerated oestrous cycle)^{8,9}. When females are faced with these events they have behavioural options or counter strategies to avoid infanticide, such as moving to an alternative location outside the new male's territory or staying to defend their cubs from attacks^{10–12}. Moving to an alternative location and avoiding the male could likely lead to resettling in inferior habitat³, or enhance the chances for injury and death if they have to repeatedly defend their cubs from the males. These consequences on the impacts of population dynamics have been rarely considered by biologists, partly due to the rare opportunities to document this behaviour in the wild^{4,10}.

Some records of females trying to avoid sexually selected infanticide (i.e. when an immigrating male, which is not the father of dependent cubs, may gain increased mating success by killing the cubs) have been documented for lions⁴ (*Panthera leo*), brown bears¹⁰ (*Ursus arctos*) and jaguars¹³ (*Panthera onca*), but similar data for tigers (*Panthera tigris*) are limited to anacedontal observations^{14,15}. We report here the responses of two female tigers to incoming immigrant males in order to avoid infanticide.

The Ranthambhore Tiger Reserve (RTR; $25^{\circ}54'N-26^{\circ}12'N$ and $76^{\circ}22'E$ to $76^{\circ}39'E$) is situated in the semiarid part of western Rajasthan and is characterized by a subtropical dry climate with four distinct seasons: summer (March–June), monsoon (July–August), post-monsoon (September–October) and winter (November–February). The study area has been described in detail by Singh *et al.*¹⁶.

The tiger population in RTR is composed of <30 individuals in the past five years^{17,18}. We monitored the tiger population through camera traps (1 camera trap/km²) and direct observations in 233 km² of the core area in RTR from April 2005 to June 2011 (refs 16, 19-22). We identified the distribution and home ranges of individual male and female tigers and recorded population and reproductive parameters (i.e. inter-birth interval, dispersal, litter size, age of first reproduction)^{16,19–22}. Besides monitoring individual tigers by camera trapping, we also used information on tiger movements by intensive searching with the Forest Department and direct sighting. If we found tigers (inside or outside RTR) involved in conflicts with humans, including killing livestock near human habitations and attacking people, we photographed them directly or with camera traps. We identified each tiger by matching its stripe patterns with the tiger photo database of RTR at the Wildlife Institute of India (WII), Dehradun¹⁶. We marked the locations of tigers using a handheld GPS device and plotted their locations in the GIS domain using the ArcView 3.3 software package (ESRI, Redlands, California, USA). We calculated the aerial distance between the plotted locations. We observed the behaviour of three tigers (one dominant male (TM-12); one resident female (TF-13) and one incoming male (TM-24)) during our study period. The home range of all three tigers was calculated using the Home Range Extension in ArcView 3.3 to generate minimum convex polygons (MCPs)²³ utilizing 100% of locations. We estimated the home range of individuals that were encountered at least three times at different locations during the study period using the MCP method, because a minimum of three points are needed to make a polygon. Additionally the open, thorny, deciduous forest with scanty vegetation and a good road network in RTR provide ideal conditions for tiger sightings. We recorded additional

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Figure 1. Distribution of three tigers in Ranthambhore Tiger Reserve, western India, 2008 to 2010.

information about the behaviour (i.e. mating, scent spraying, territorial marking, fight, prey hunting, rearing of cubs) of male and female tigers.

In one case we observed that the female (TF-13) with two cubs moved to a new area after the disappearance of the dominant male tiger (TM-12). Before its disappearance the male's range covered the home range of the female (Figure 1). In August 2008, female (TF-13) delivered two cubs (M, F) and reared them until they dispersed. Subsequently, after 2 years, in August 2010, TF-13 was photo-captured with two cubs (unknown sex). Because the male and female shared the same home range, both litters were likely the progeny of the male TM-12. After the emigration of male TM-12, the vacant home range was acquired by another immigrant male (TM-24). Evidence of this was confirmed by our regular monitoring of tigers using camera traps (October 2010, adult male TM-24 (> 3 years) was photo-trapped within the territory of TF-13). This male tiger had been previously physically captured approximately 4 km away in a suboptimal habitat²⁴. To possibly avoid infanticide, the female moved her cubs to a new area approximately 20 km away in riverine areas (Figure 1). The female (TF-13) and cubs were confirmed by photographic evidence through camera traps (December 2010) in the riverine area. Both the female and the cubs were monitored continuously using camera traps until the following monsoon (August 2011).

Our results highlight the response of a female tiger with cubs (<6 month) to an immigrating male, including avoidance of the new male. After the arrival of the new male, the female left her established territory in which she had successfully reared previous cubs. Similar female strategies to avoid infanticide have been observed in several species (felids, primates and captive rodents), thus providing a mechanism whereby females may reduce their losses to infanticide¹⁰. A few records of infanticide have also been reported in tigers at the Kanha Tiger Reserve, India (M. S. Panwar, unpublished) and Chitwan National Park, Nepal^{14,15,25}. Sunquist²⁶ also observed immigration of males after the death of a dominant male tiger, which lead to fighting among them, and there was no breeding for two years.

In another case we observed a female (TF-04) with cubs vigorously attacking (2 April 2009) an intruding male and successfully defending her cubs. The day after the fight the female succumbed to injuries. The postmortem report confirmed that the animal died due to deep canine injuries in her skull and neck. This could be the immediate response of mothers against intruding males to prevent conspecifics from killing their offspring^{10,11}.

This study has recorded the response of a female tiger to an immigrating male to likely avoid infanticide in a semi-arid region in western India. This information is important to better understand the behaviour of an endangered species towards probable infanticide and factors that can govern their conservation implications.

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Resource allocation within the replacement clutch: do female European starling (Sturnus vulgaris Linneus) adjust their reproductive strategy after a full clutch loss?

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An important factor in the evolution of reproductive strategies in birds is the loss of a clutch or a brood. Many avian species produce a replacement clutch following the loss of the first clutch, but additional breeding effort carries physiological costs and can also reduce female fitness. Thus, egg production in replacement clutches is usually reduced. In contrast, European starling mothers seem to invest equally in their first and replacement clutches. This study investigated whether female starlings use differential allocation of resources to offspring, rather than egg production, to strategically balance investment and

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