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Can antler stage represent an activity driver in axis deer *Axis axis*?

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The aim of this study was to determine the seasonal activity patterns and asynchrony between different antler stages in male axis deer from the Mediterranean island of Rab in Croatia using camera traps. Nine cameras with an infrared motion detection system were used to track animal activity over a 12-month period, 24 h per day. Stags were divided into two categories of antler development: regeneration stage and hard antler stage. The frequency of detection of each category in the photographs allowed us to investigate seasonal activity patterns. To describe the seasonal activity pattern in each category, we fitted the segmented linear regression and predicted that the ratio of monthly activity of stags in the two antler categories would interchange regularly during the research period. Over the 12-month study period, 36 862 photographs were analysed. A significant difference in frequency was found between the two antler categories ($p < 0.01$), with a consistently greater presence of hard-antlered stags. The highest frequency of detection of both antler categories was found in the winter season, and the lowest in spring. The segmented linear regression clearly distinguished three break points in April, June and December in the hard antler stage, with a significant difference in activity pattern among the months for each slope. On the other hand, no significant difference was found for the regeneration stage. Therefore, the expected proportional interchange in the number of stags in the two antler stages throughout the year did not occur. This study revealed that the Mediterranean axis deer population showed a unique activity pattern, where antler stage may act as a possible driver regulating stag movements.

Keywords: activity pattern, antler development, camera traps, Mediterranean, tropical deer

The antler cycle is closely linked to the testicular cycle and the associated seasonal fluctuations in androgen secretion in male deer (Price et al. 2005, Ramesh et al. 2013). Antler growth occurs during the period of low testosterone concentration, whereas antler mineralization and velvet shedding from antlers are spurred by increasing testosterone levels and corresponding increase in mating activity (Lincoln 1992, Bubenik 2006). Casting of antlers is triggered by a marked decline in testosterone levels, which can occur at various rates, depending on the sex ratio within the respective population. Antlers are the only body appendages in mammals to undergo full regeneration (Goss 1983).

Growth of antlers in cervid species from temperate areas is a seasonal event occurring every year in close synchronicity with photoperiod (Goss 1983, Sempéré 1990). Antlers are cast and re-grown from the top of the pedicles, permanent frontal protuberances covered with normal scalp skin (Kierdorf and Kierdorf 2011). The age of first development of the pedicles depends on nutrition status and body mass (Sempéré 1990, Price and Allen 2004). The onset of antler formation on top of the pedicles is indicated by the appearance of velvet, a specialized integument rich in sebaceous glands and with hair lacking arrector pili muscles (Goss 1983, Bubenik 1993). After velvet shedding, antlers appear as completely bony structures (Goss 1983, Ramesh et al. 2013). The size and complexity of antlers increase with increasing body size and age of individuals (Bubenik 1990). Accordingly, antlers play a primary role in defining social structure in male deer, as they are used as display weapons in intra-sexual combat (Clutton-Brock 1982), and their size correlates positively with dominance (Lincoln 1972). In fact,

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upon casting antlers, dominant stags in red deer *Cervus elaphus* are almost challenged by one or more subordinate stags and often displaced from the group. A similar pattern was shown to occur also in moose *Alces alces*, elk *Cervus canadensis* and caribou *Rangifer tarandus* in a 'dummy antler' experiment (Bubenik 1983).

Seasonal fluctuations of climatic and environmental conditions are the key drivers that shape the reproductive cycle (including mating activity) in cervids (Bubenik et al. 1986, Foley et al. 2015). Unlike boreal deer species, which are strictly seasonal breeders, axis deer *Axis axis* reproductive cycle is closely related to the species' adaptability to a wide range of environments (Willard and Randel 2002) and their tropical origin with comparatively minor annual changes in photoperiod (Loudon and Curlewis 1988). Although photoperiod is the dominant environmental cue that entrains the seasonal antler cycle in deer from temperate regions (i.e. seasonally breeding deer; Feldhamer and McShea 2012), in tropical (axis) deer, Loudon and Curlewis (1988), suggested that photoperiod is not involved in controlling the antler cycle. Reproductive cycle and the antler cycle of tropical deer species such as axis deer appears to be aseasonal in most of their native habitat (tropics) and depends on the availability of food, which is determined by local climatic conditions (Fraser-Stewart 1985). Depending on the environmental conditions, the mean interval from casting to casting in axis deer from tropical regions ranges from 45 to 60 weeks, with the duration of the hard antler stage from 23 to 37 weeks and 17 to 30 weeks from the casting of the old antler to the cleaning of velvet (Loudon and Curlewis 1988, Bubenik et al. 1991, Lincoln et al. 1998). However, in subtropical regions axis deer may exhibit seasonality with relatively good synchronization of the antler cycle (Bubenik et al. 1991). As a result, mating activities that influence monthly and seasonal changes in axis deer group size (Raman 1997) show great variations among populations across various ecological contexts (Schaller 1967, Šprem and Zachos 2019), thus affecting activity patterns of male axis deer individuals in different antler development stages. Although seasonal dynamics of mating activity in axis deer remain unexplored, there are few studies describing activity patterns of this species (Schaller 1967, Dave 2008, Centore et al. 2018). By taking into account the above-mentioned, antler stage can allow to predict phase of reproductive cycle.

Axis deer originating from the Indian subcontinent have been successfully introduced to Croatia twice, though the exact provenance of the introduced individuals is unknown (Kusak and Krapinec 2010, Frković 2014). In 1974, seven individuals were released on the Kalifront Peninsula of the island of Rab and preserved ever since for hunting purposes (Tomljanović 2016). The axis deer from the Adriatic Islands in Croatia are the only free-ranging European populations (for more details see Šprem and Zachos 2019).

Taking advantage of the atypical (i.e. non-native) ecological conditions of the extant axis deer populations in Croatia, we aim to investigate the seasonal asynchrony in the antler cycle and seasonal activity patterns of male axis individuals in different antler stages using camera traps. Owing to the scarce data available on the antler phenology in axis deer

in different ecological contexts (Schaller 1967, Mishra and Wemmer 1987, Waring 1996), if the seasonal activity pattern of individuals in different stages is related to the antler cycle, we expect that:

- 1) seasonal activity pattern will vary between individuals in different antler stages, with the highest occurrence of stags in the hard antler stage expected in the expressed rutting periods: January–February, July–August and October–November (Šprem et al. 2008);
- 2) the ratio of individuals in different antler stages will be unbalanced throughout the year and should regularly interchange between consecutive months, i.e. the higher occurrence of stags in the hard antler stage during rutting periods will be replaced by a higher occurrence of stags in the regeneration stage in other periods.

Material and methods

Study area

The study was conducted on the northwest side of the island of Rab, in the northern Adriatic Sea in Croatia (Fig. 1). Owing to the climate and geological conditions, scrublands and woodlands of Euro-Mediterranean vegetation dominate. The area is a forest ecosystem composed of carbonate rocks with predominant holm oak *Quercus ilex*, and manna ash *Fraxinus ornus* cover (Ugarković and Ugarković 2013), at elevations between sea level and 94 m. Forest cover prevails (94%; Tomljanović 2016), with stem density (733–9581 ha⁻¹) in the study area (Oršanić et al. 2011). According to the Köppen classification, the study area belongs to Cfa climate group of humid subtropical climates (Seletković et al. 2011), with an average annual temperature of 15.3°C (mean temperature: 23.6°C in summer; 8.0°C in winter). The vicinity of a continental montane region strongly affects the study area, characterized by the maritime rainfall regime (annual precipitation 1102 mm). However, the area is considered one of the sunniest places in Europe, with an average of 2479 sunshine hours per year, coupled with an extremely dry period from mid-June to August. Highly nutritional low vegetation forms (various grasses and herbaceous plants) develop in early spring (April and May). Large herbivores in the study area during the 2015/2016 season were axis deer (n = 78; 9.2 ind. 100 ha⁻¹) and European mouflon (n = 103; 12.2 ind. 100 ha⁻¹) (Centore et al. 2018). According to the estimates in the present management plan, the sex ratio ranges between 0.86 and 1 in favour of females, and the age structure is: 19% juveniles, 18% yearlings and 63% adults (Tomljanović 2016). Mating and calving in axis deer occurs year round and there is no strictly defined mating season, therefore stags can be found in various stages of antler development regardless of season (Šprem et al. 2008). Most of the time, adult males are separated from the herds consisting of females with calves (3–10 individuals) or young males (3–5 individuals). During the rut, males rarely fight, whereas subadults and males with growing antlers avoid the rutting areas (Šprem and Zachos 2019).

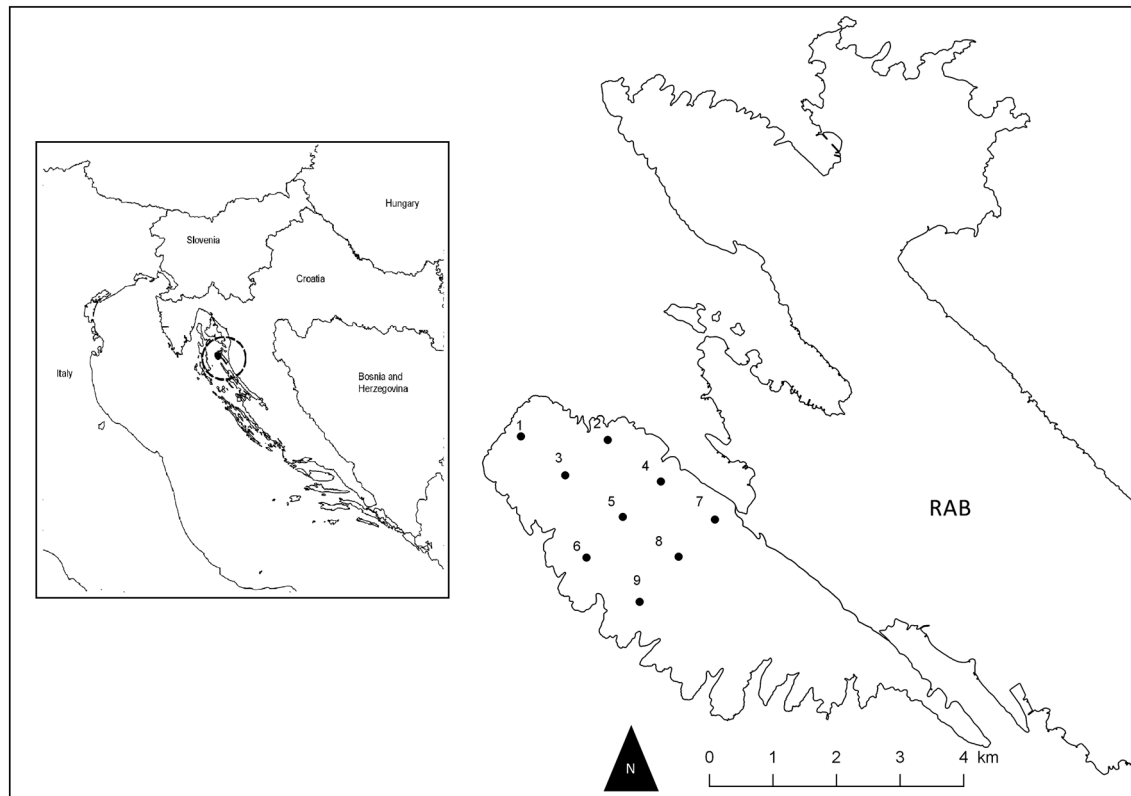


Figure 1. Study area of the island of Rab in the northeast Adriatic Sea, and Kalifront Peninsula showing the nine camera trap locations.

Data collection

Camera traps are increasingly used to observe the behaviour patterns of individuals, estimate population abundance and identify sex and age where possible (Anile and Devilard 2018). Moreover, daily or seasonal activity patterns of wild animals can be investigated using metadata information (time and date of caption, Frey et al. 2017) alongside the frequency of detections (Green et al. 2015, Bu et al. 2016). Data were obtained using camera-traps (Wildlife Innovation, Spypoint models: Iron, PRO-X, HD-12, Moultrie models: MFH-DGS-D55IR, MCG-12589 and Primos Truth Cam 35 infrared detection game cameras) between 1 April 2015 and 31 March 2016. A systematic net grid of 1000×1000 m was set and cameras placed at each grid intersection, covering an area of approximately 90 ha. For this purpose, nine cameras were placed from 50 to 100 cm above ground level, with a 5-min delay between consecutive photos and a default focus distance of 5 m. Cameras were active 24 h per day and checked twice a month to collect photographs and check battery status.

Data analysis

To obtain actual information on antler status, all photos from the nine cameras were pooled, since the population range is restricted by island size and habitat usage is evenly distributed across the study area. Only photographs clearly showing stags were used. Photographs were categorized by month (from January to December).

Since the new set of antlers begins to grow almost immediately after the old ones are shed (Schaller 1967), we

combined stags without antlers and those with antlers in velvet to reduce the bias when making conclusions about the activity patterns of stags in the antler growth period. Therefore, the antler stages were divided into two categories: regeneration stage and hard antler stage, taking into account the average duration of these categories in other studies (Loudon and Curlewis 1988, Lincoln et al. 1998). All male age classes were pooled, since it was impossible to properly estimate age based on the antler development (Gee et al. 2013, Ikeda et al. 2013). Frequency of detection of each category in the photographs allowed us to investigate the seasonal activity patterns (Green et al. 2015, Bu et al. 2016). Accordingly, to examine the differences between the frequency of detection of antler categories on camera traps, the Student's t-test was used, where only presence (1) or absence (0) of each category in the same photograph was recorded. The presence of stags without antlers allowed for an estimation of the peak of casting periods.

To detect the finer scale of antler transformation, based on irregular growth patterns of axis deer antlers, each individual captured in the same photograph was treated as a single observation and associated to one of the two categories. To describe the activity pattern of each category (i.e. including the total number of individuals counted, belonging to one of the two categories), we fitted segmented linear regression models with month as a predictor variable for each antler category, using the R package 'segmented' (Muggeo 2008). The package offers facilities to estimate and summarize generalized linear models with segmented relationships without any limit on the number of segmented variables or the number of change points. The activity pattern of each category was compared using breakpoints and slopes.

Finally, we predicted that the ratio between hard antler stage and regeneration stage will regularly interchange during the study period. All statistical analyses were performed using R ver. 3.3.2 (<www.r-project.org>) in RStudio, ver. 1.1.423 (RStudio Team 2016). All parameter estimates were reported with standard errors (SE).

Results

During the 12-month study period, 122 082 JPEG photographs were collected, and 36 862 were selected according to the above criteria for analysis. We found significant differences in the frequency of detection of axis deer stags between two antler categories (regeneration stage versus hard antler stage; t-test: $t = -6.3208$, $df = 11$, $p < 0.001$). The highest frequency of detection was found for both antler categories in the colder part of the year (i.e. November, December and January) (Fig. 2), particularly in November, with 2694 counts of stags in the hard antler stage and 1304 counts of stags in the regeneration stage. In contrast, the lowest frequency of detection was recorded in May for stags in the hard antler stage (406 counts), and in June for stags in the regeneration stage (148 counts) (Fig. 2). Furthermore, the highest peak of antler casting occurred in November (546), with two smaller peaks in April (117 counts) and August (241 counts) (Fig. 3).

With reference to the total number of recordings in each antler category, the segmented linear regression in the hard antler stage clearly distinguished three break points (Fig. 4), in April (estimate = 4.53), June (estimate = 6.79) and December (estimate = 10.21). The first decrease in the frequency of hard antler stage occurred from December to May (slope 1: estimate = -802.3, SE = 46.612, $t = -17.212$, $p < 0.01$), followed by an increase from May to July (slope 2: estimate = 808.0, SE = 147.4, $t = 5.4817$, $p < 0.01$) and from October to December (slope 4: estimate = 756.0, SE = 147.4,

$t = 5.128$, $p < 0.01$). No significant change in frequency was found from July to October (slope 3: $p > 0.05$) (Fig. 4). Comparatively, in the regeneration stage, segmented linear regression distinguished only two break points in May (estimate = 5.83) and July (estimate = 7.02), without a significant difference in frequency between months for each slope (Fig. 4).

Discussion

The aim of this study was to provide insight into the antler phenology of a Mediterranean island population of free-range axis deer. To the best of our knowledge, this unique study provides a first review on seasonal activity patterns of axis deer stags in different antler stages in Europe. The camera trap survey distinguished three periods of antler casting, with the highest portion of stags without antlers occurring in November (Fig. 3), thus suggesting a conspicuous reproduction shift with an increasing percentage of stags in the regeneration stage from September to November (Fig. 5).

In deer, the testosterone cycle is responsible for regulating the antler cycle and synchronizing it with the reproductive season (Rolf and Fischer 1996). As recorded by Šprem et al. (2008), matings of axis deer in the Mediterranean region can be observed in January–February, July–August and October–November. Hence, looking at the frequency of detection of stags in the hard antler stage in this study, the results indicate a similar mating pattern in line with those proposed in our hypotheses, though it is evident that mating occurs year round. In Nepal, for example, the peak period of hard antlers occurs once a year in May and coincides with the peak period of the rut when the sexes mixed (Mishra and Wemmer 1987), which is remarkably different than found in this study. Information about the activity patterns of axis deer antlered males is lacking, and findings concerning antler cycles vary. Observations conducted in India, for exam-

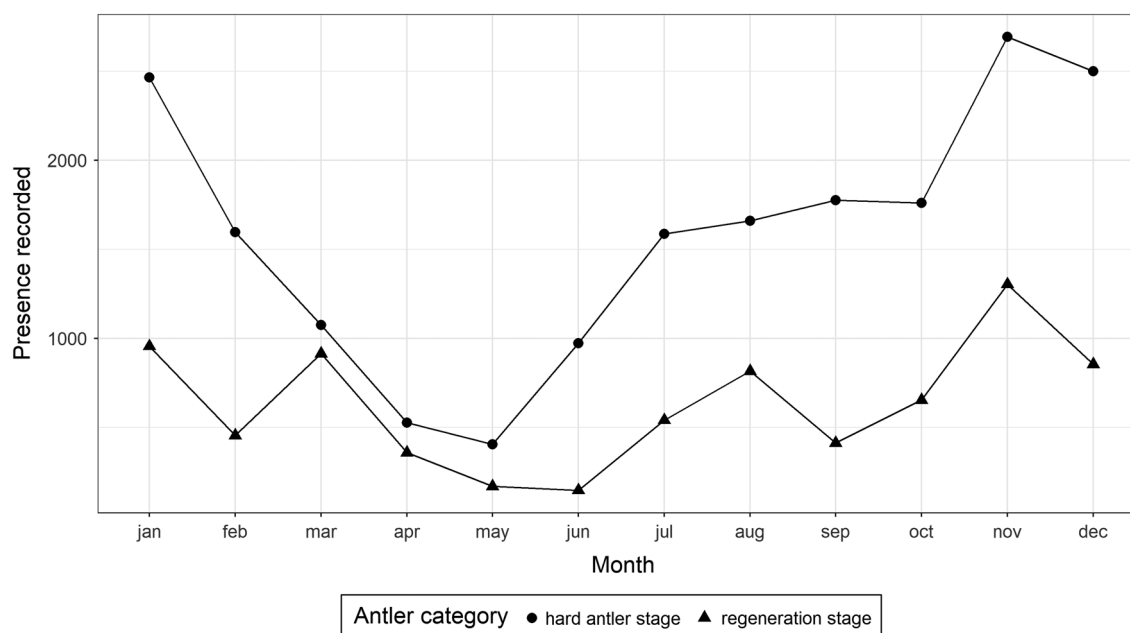


Figure 2. Number of records in each month of axis deer stags in hard antler and regeneration stage on the island of Rab.

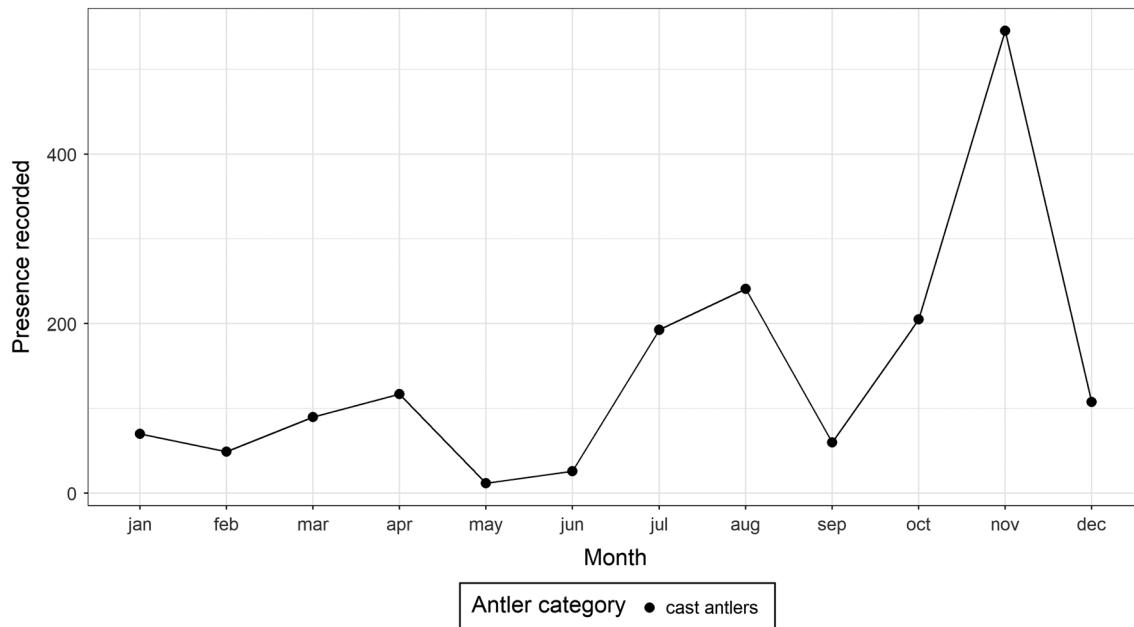


Figure 3. Number of records in each month of axis deer stags with cast antlers on the island of Rab.

ple, showed contrasting patterns, with a high frequency of hard-antlered males (82.2%, Miura 1981) or a prevalence of velvet stags from February to April (Waring 1996), December to February (Mishra and Wemmer 1987), and the occurrence of a transition phase from velvet to hard antlers in March (Schaller 1967).

The occurrence of stags in both antler stages was lowest in the early spring, suggesting an apparent decrease in the level of activity. Similarly, a recent study by Centore et al. (2018) recorded the lowest activity of axis deer (all age and sex categories) in spring on the island of Rab. This may relate to the peak of productivity of low vegetation layers, especially grasses in April and May, which constrained foraging activity to pastures. This constraint supports previous findings that showed how grasslands were used preferentially by axis deer in lowland Nepal in February, March and April (Moe and Wegge 1994). Unlike continental areas, the Mediterranean

region has unfavourable conditions for ungulates in summer due to high temperatures and drought. Consequently, in this period animals are forced to move and increase their search for food. In late June and early July (after the grazing period in spring), axis deer on the island of Rab preferred one-year shoots of woody species (Krapinec et al. 2000). Indeed, the present study found a gradual increase in the frequency of both categories, starting in June and reaching its peak in November, suggesting a marked change in the activity pattern across seasons (Fig. 2).

In particular, the results indicate that antler stage may be an important driver of deer activity during the year, as confirmed by the consistently lower frequency of detection of stags in the antler regeneration stage. Consequently, the expected proportional interchange in the number of stags in different antler stages throughout the year did not occur (Fig. 5). In contrast, in their native habitat in Nepal, axis deer

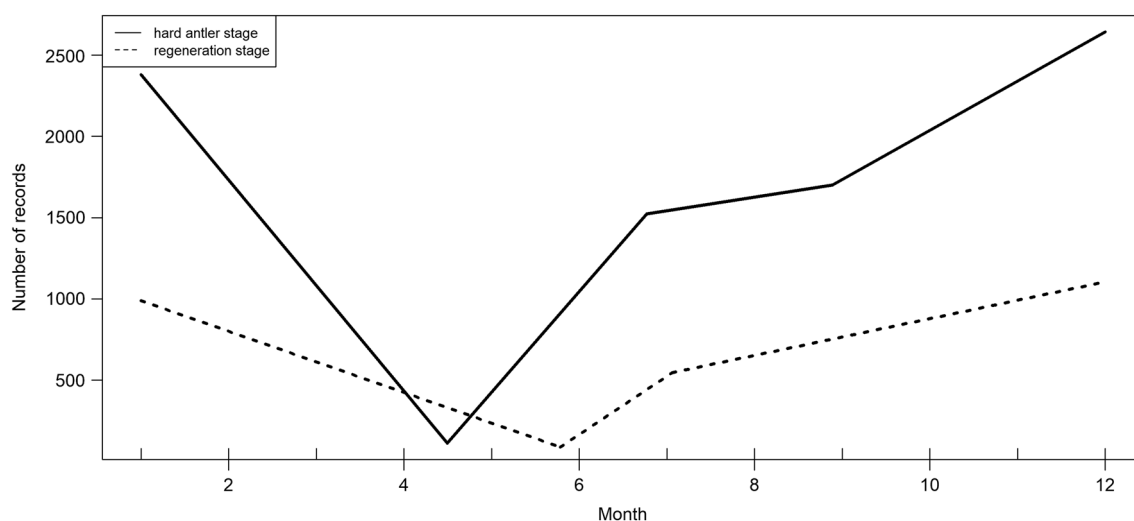


Figure 4. Regression model with segmented relationship of two antler categories (hard antler stage-solid line and regeneration stage-dotted line) showing different seasonal activity patterns.

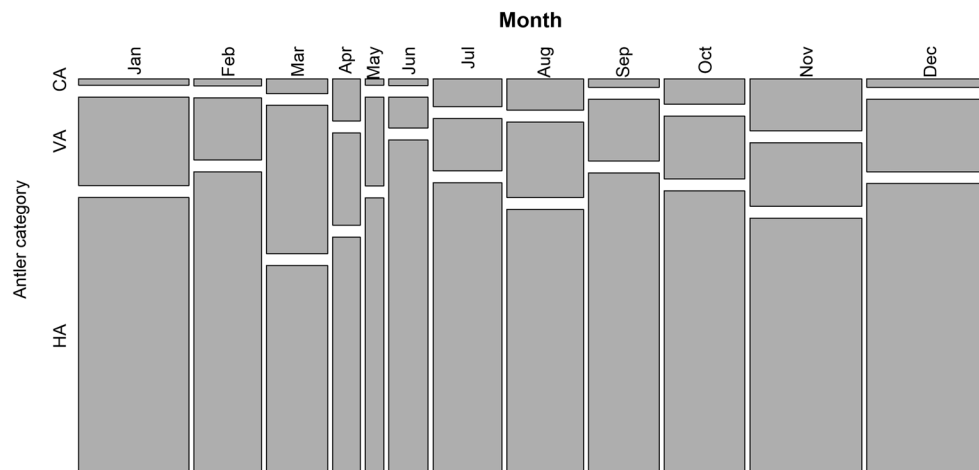


Figure 5. The ratio of individuals in different antler stages on the island of Rab – column width indicates the total number of stags recorded (HA – hard antler stage, VA – velvet stage, CA – antler casting).

showed a clear interchange during the season in the percentage of stags in the velvet and hard antler stages (Mishra and Wemmer 1987). We acknowledge that the duration of the period between the hard antler stage and the regeneration stage should be accounted for in the analysis, as it showed conspicuous variations among individuals in previous studies (23–37 weeks hard antlers, 17–30 weeks regeneration phase; Loudon and Curlewis 1988). Unfortunately, such information is lacking for this island population, though the higher frequency of detection of individuals in the hard antler stage during the season could be partially explained by a longer duration of this stage. On the other hand, sexual competition in deer species during the breeding season can cause dispersal among males (Jarnemo 2011) and it is possible that the hard-antlered axis stags showed increased mobility while searching for females in heat, which may be reflected in the higher frequency of captures. However, breeding dispersal is primarily driven by strong competition for mating and overt aggression (cf. Rosenberry et al. 2001), which are not expressed in the sexual behavioural patterns of axis deer (Mishra and Wemmer 1987, Šprem and Zachos 2019).

Growing antlers are very sensitive and the slightest pressure may cause pain, bleeding and even disfigurement of the (still) soft bone surface (Caton 1877, Whitehead 1972). Consequently, deer in velvet tend to avoid contact between antlers and other objects (Whitehead 1972). In turn, velvet stags living in dense forest habitats may show a decrease in activity to avoid contact with dense vegetation (Tomljanović 2016). Moreover, since the period of rut is not fixed, and mating occurs year round, it is possible that stags in the regeneration stage avoid clashing antlers with hard-antlered stags, thereby restricting their movement.

In conclusion, the present study showed that the Mediterranean island population of axis deer display a unique activity pattern, with antler stage as a possible driver regulating stag movements. Certainly, restricted habitat use raised the possibility of direct contact between individuals and shaped their movement patterns. However, the effect of environmental conditions and related food availability should not be neglected as one of the foremost activity drivers. To support our claims, future analysis of movement

and habitat use from telemetry data in relation to habitat conditions is required.

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