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Sequential predictability of the scanning behaviour of greater rheas, *Rhea americana*

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Some models that predict the scanning pattern to maximise the probability of predator detection by prey assume sequential randomness (i.e. lengths of inter-scan intervals are independent of each other and of the length of scan events). Sequential randomness would prevent stalking predators synchronising their attacks with long inter-scan intervals. We analysed the presence of sequential randomness in the scanning behaviour of the greater rhea (*Rhea americana*), a large flightless bird that forages solitarily or in groups. We analysed sequences of behaviour of 40 wild rheas, foraging solitarily or in groups of 2 to 17 individuals, in two populations in eastern Argentina. We used parametric (auto and cross-correlations) and non-parametric (runs and Spearman rank correlation) tests to detect dependence among intervals. We detected the temporal dependence of inter-scan intervals in 30 of 40 behavioural series, but only 11 of 40 sequences showed consistent dependence when tested using parametric and non-parametric tests. The temporal dependence detected in some individual sequences would still be used by predators to synchronise their attacks with long inattentive periods of the prey. However, simple simulations showed that attack success would not be different from that of predators launching their attacks at the beginning of a randomly selected inattentive period of the prey. We propose that temporal dependence among the length of inattentive periods in greater rheas would be the result of simple mechanistic rules determined by the compromise between foraging and scanning behaviour, and it would be of little value to potential stalking predators.

KEY WORDS: greater rhea, *Rhea americana*, scanning pattern, predation, sequential randomness.

INTRODUCTION

Vigilance is one of the behavioural defences that prey uses to detect and avoid predators (CARO 2005). Several models have been developed to predict individual

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scanning behaviour by prey that maximises their probability of survival. These models assume that the scanning pattern should be unpredictable for predators to prevent them synchronising their attacks with unattended periods of prey (Pulliam 1973; Bertram 1980). Unpredictability in vigilance behaviour would be the result of two basic mechanisms: (1) scan events are produced at random (*instantaneous randomness*); and (2) the length of an inter-scan interval (time between consecutive scan events) is independent of the previous one (*sequential randomness*; see Bednekoff & Lima 1998 for a review). Uncorrelated inter-scan intervals may make the synchronisation of an attack difficult because the predator cannot predict when a long unattended period will happen. Studies that tested whether animals scan randomly and whether inter-scan intervals are independent of each other have obtained opposite results. Random scans have been described in ostriches, *Struthio camelus* (Bertram 1980), but other studies observed a non-random pattern of scanning (e.g. Lendrem 1983; Hart & Lendrem 1984; Sullivan 1985; Lendrem et al. 1986; Beauchamp 2006; Carro & Fernández 2009). Further, some theoretical models did not support the view that random scanning is the optimal strategy for detecting an approaching predator (Scannell et al. 2001; Bednekoff & Lima 2002). Similarly, support for the sequential independence of inter-scan intervals is controversial, as some studies reported the presence of sequential randomness (Roberts 1994; Suter & Forrest 1994), while others described the occurrence of periodicity (and therefore, predictability) in the scanning sequences of individuals (Desportes et al. 1989; Ferrière et al. 1999). Despite possible differences in the methods applied to analyse sequences (see Bednekoff & Lima 1998), most authors agree that the lack of sequential randomness could be used by predators to time their attacks.

Predictability in behavioural sequences has been attributed to group-level coordination of vigilance (Ferrière et al. 1996, 1999). According to this interpretation, individuals in a group are able to predict the sequences of vigilance of their neighbours to synchronise their behaviours, increasing coordinated vigilance while reducing coordination costs (see Ferrière et al. 1996, 1999). However, most studies of sequential randomness involved the analysis of behavioural sequences of one or a few solitary individuals (Desportes et al. 1989; Roberts 1994; Ferrière et al. 1996; Ruxton & Roberts 1999; but see Beauchamp 2006; Barros et al. 2008). If periodicity in the scanning behaviour tends to increase coordination, it should be more easily detected in large groups than in solitary individuals or small groups.

Temporal non-random patterns in the scanning sequences have also been attributed to changes in external conditions, such as group size, food distribution, or predation risk (Roberts 1995; Ruxton & Roberts 1999; Beauchamp 2006; Barros et al. 2008). Changes in group size and differences in local food abundance can produce short-term changes in scanning behaviour that result in short-term predictability (Roberts 1995; Beauchamp 2006), while differences in predation risk can generate short-term and long-term differences in the scanning pattern of potential prey (Ruxton & Roberts 1999; Barros et al. 2008).

In this study we analyse the occurrence of sequential randomness in the scanning behaviour of 40 greater rheas (*Rhea americana*) foraging solitarily or in groups of 2 to 17 individuals. We assessed whether temporal dependence is present in the rhea's scanning behaviour and analysed social and environmental effects on individual scanning behaviour. We also explored the consequences of the greater rheas' scanning predictability on the risk of predation that they might experience. We specifically tested whether the length of inattentive periods of individual sequences can be predicted from the length of the previous scan or inter-scan events, and whether departures from predictions are associated with sex or group size. We also tested whether habitat structure affects the scanning pattern of greater rheas by comparing the behaviour of individuals inhabiting two different sites. We expected that the scanning behaviour of greater rheas at the site with higher vegetation cover would have less regularity, as potential stalking predators might use cover to make a more effective and closer approach and use such regularities to time their attacks. Finally, we used a simple simulation model to assess the effect of temporal dependence on the risk of predation.

METHODS

Study species

Greater rheas are large (20–30 kg in mass), non-flying birds that inhabit open habitats in South America, from the north of Brazil to the north of Patagonia in Argentina. They are a gregarious species that form groups of 2 to 20 or more individuals, although some individuals (mainly males) can remain solitaries. The typical group size for open habitats in Argentina is 7.6 individuals (Carro & Fernández 2008). They are herbivorous birds that feed on forbs and grasses in open fields, although they can also eat invertebrates and small amphibians (Martella et al. 1996; Davies 2002). Previous studies have shown that greater rheas decrease the time spent in vigilance as group size increases (Martella et al. 1995; Reboreda & Fernández 1997; Fernández et al. 2003), and that the production of scan events departs significantly from random (instantaneous randomness), resulting in longer inter-scan intervals than expected (Carro & Fernández 2009). In at least one of the previous studies (Reboreda & Fernández 1997), males were more vigilant than females.

General procedure

We analysed behavioural sequences of individual wild greater rheas at two sites: Gualeguaychú, in Entre Ríos Province, Argentina (33°01′S, 58°24′W), hereafter site 1, and General Lavalle, in Buenos Aires Province, Argentina (36°25′S, 56°56′W), hereafter site 2. Data from site 1 were collected during the non-breeding seasons (April–August) of 1991 and 1992, while data from site 2 were collected during the non-breeding seasons of 1995, 1996 and 1999. Site 1 is open grassland with scattered patches of bushes and trees, while site 2 consists of highly homogeneous pastures. Both sites are grazed mainly by cattle. At present, there are no natural predators of adult rheas (i.e. cougars, *Felis concolor*) in these areas, but at both sites they are hunted by feral dogs and occasionally by humans. Although both sites are open grasslands, higher cover and the presence of patches of bushes and trees make site 1 an a priori more risky habitat for greater rheas, as potential stalking predators might use vegetation cover to make a more effective approach and attack.

Individuals were either video-recorded with a Sony Hi8 camcorder (Sony Corporation, Tokyo, Japan) or observed with binoculars from inside a vehicle at distances of 100 to 200 m. Records involved solitary individuals and individuals in groups from 2 to 17 adults. We considered that greater rheas were in the same group when they were less than 50 m away from one another. Group membership changes as individuals can leave one group and join other groups freely. However, this rarely occurred during our observations and in the few cases in which this happened we stopped the recording. Data were collected in a different place each day. As birds were not marked and moved freely within the study area, we cannot rule out having recorded the same bird more than once. However, if this happened, it was on a different date or at a different place. The video-recording started 15–20 min after arriving at the place where the birds were foraging. Data were collected from 07:30 to 19:30. Each recording ended after 15 min or when the target animal moved out of sight. Recording of less than 3 min were excluded from the analysis.

Data analysis

We analysed the behavioural sequences of 40 animals, 21 from site 1 (19 males and 2 females) and 19 from site 2 (15 males and 4 females), that foraged solitarily or in groups of 2 to 17 animals. These individuals did not show aggressive, preening, resting or courtship behaviours during the observations (see CARRO & FERNÁNDEZ 2008 for a definition of these behaviours) and their behavioural sequences fitted the minimum requirements for time series analyses (see below). We timed different behaviours using an event recorder program (Etholog 2.5.5) to the nearest 0.1 sec. We defined two mutually exclusive behavioural categories: scan (vigilance) and inter-scan. We considered that a greater rhea was vigilant when it stood with its head up (see REBOREDA & FERNÁNDEZ 1997). Inter-scan behaviours included other behaviours, such as walking and feeding. Feeding and vigilance accounted for about 80–90% of the time budget during daytime (REBOREDA & FERNÁNDEZ 1997). Therefore, the sum of inter-scan and scan intervals represent the total time the individual was observed.

We analysed the temporal dependence of inter-scan intervals (hereafter ISI) within behavioural sequences using autocorrelation tests. In these tests we assessed the k-order correlated dependence among the i and $i–k$ intervals of the temporal series for $k = 1$ to $k = 6$ (BOX & JENKINS 1976; ROBERTS 1994). We previously checked whether ISI and scanning events in the behavioural sequence have constant mean and variance along time (stationarity criteria), as an increase or decrease of these values along the series would result in spurious correlations (BOX & JENKINS 1976). We used the Dickey–Fuller test to check for stationarity in each registered series and excluded those that showed some temporal trend. Only stationary series were included in the subsequent analyses.

The dependence of the length of ISI on the length of the previous scan (hereafter SI) in the same behavioural sequence was analysed using cross-correlation tests considering delays of $k = 0$ to $k = 6$ between the ISI and the previous scan events ($k = 0$ the immediately previous scan event).

We applied auto- and cross-correlations to stationary temporal series with 20 or more ISI events. However, because the low number of scan/non-scan transitions could affect the results of parametric tests (BOX & JENKINS 1976; ROBERTS 1996), we repeated the analysis using non-parametric one-sample run tests (SIEGEL & CASTELLAN 1988). This test was used to assess whether long (> median value of ISIs) or short (< median value of ISIs) ISIs occurred together in the sequence more often than expected by chance. We also used Spearman rank correlations to assess the association between the lengths of ISI and the immediately previous SI.

Short temporal series could also show temporal dependence by chance. To test this possibility, we randomly rearranged the original sequences of ISI and SI in the series that showed temporal dependence and repeated parametric and non-parametric tests on these new re-arranged sequences to check for correlations. We repeated this rearrangement of series 100 times for each original series to obtain a distribution probability of detecting temporal dependence by chance. We considered that the original series showed a genuine temporal dependence if we detected that a similar or a more extreme dependence between ISIs or between ISIs and SIs occurred in < 5% of the rearranged series.

We assessed the effects of sex, group size, and site on the occurrence of non-random sequential scanning patterns using a forward stepwise logistic regression model with occurrence of sequentially non-random pattern as a binary response. We considered that a factor had an effect on the probability of occurrence of a non-random scanning pattern if its deletion from the model produced a significant change in the fit, with an α level = 0.05 (TABACHNICK & FIDELL 1996).

We used simple simulation models to test the risk represented by the predictability in the sequences observed in wild rheas. We took sequences where we detected temporal dependences and simulated an attack of a predator that was able to use sequence predictability to time its attack. For each individual sequence, we estimated the proportion of potential attacks that were successful based on the prediction curve of t_{i+k} as a function of t_i, where t_i is the length of the interval i (SI or ISI) and t_{i+k} the length of the i+k-correlated inter-scan interval of the temporal series. When the length of the ISI of a series was related to more than one previous SI or ISI interval, we selected for the simulation the relationship with the highest determination (r) or concordance coefficient (*tau*). We selected for the attack all intervals where t_i predicted a t_{i+k} value longer than the approaching time of predator, τ. This parameter τ represents the time that a predator takes to reach a minimum distance at which the prey is unable to escape, and it is inversely related to the approaching speed of the predator (the detection threshold; LIMA 1987; BEDNEKOFF & LIMA 2002). For the simulations we used values for τ of 5, 10, 15 and 20 sec. We considered an attack as successful if the observed interval t_{i+k} was longer than τ. Predator efficiency was estimated as the proportion of successful attacks (number of t_{i+k} observed intervals $> \tau$/number of predicted $t_{i+k} > \tau$). This efficiency was compared with the efficiency of a simulated predator that launches its attack randomly (at the beginning of a randomly selected inter-scan bout) using non-parametric Wilcoxon paired-sample tests (significance was set at $P \leq 0.05$).

RESULTS

The length of inter-scan intervals varied from 0.5 to 260 sec (mean ± SE: 19.98 ± 0.01; Fig. 1(a)), while the length of scanning bouts varied from 0.3 to 38.6 sec (mean ± SE: 3.19 ± 0.002; Fig. 1(b)). Using parametric methods we found a temporal dependence of the length of the ISI on the previous ISI in 9 of 40 individual sequences (Table 1). Six of these cases were negative (long inter-scan bouts were followed by short ones or vice versa), whereas the other three were positive (long inter-scan bouts were followed by long ones and short inter-scan bouts by short ones). However, determination coefficients of correlations were relatively low (mean = 0.43, range 0.33–0.51; Table 1). Non-parametric tests showed that in 7 of 40 individual sequences, ISIs were produced in a non-random sequence. Furthermore, all 14 series in which we detected temporal dependence among ISIs did not appear to be the product of chance, as fewer than 5% of the randomly rearranged series showed a temporal dependence more extreme than the empirical sequences. However, rearrangement of 8 series showed temporal correlations among ISIs of different order from those observed in the original series (> 5% of simulations). Considering parametric and non-parametric tests and exact probabilities calculated from rearranged series, only 2 series showed consistent temporal dependence. These results do not provide evidence of the existence of predictability generated by ISI–ISI dependence in the greater rhea vigilance pattern. Overall, only 9 out 520 tests performed over the total individual sequences showed a significant relationship among ISIs (1.7% of tests), a value lower than expected by chance (5%).

When we considered the relationship between the length of the scanning bout and the length of the subsequent non-scanning bout, predictability was higher. According to parametric tests, 17 of 40 individuals showed a significant correlation between the length of the scanning bout and the length of the subsequent ISI (Table 1). Fourteen of these sequences showed a positive relationship (long vigilance bouts were associated with long ISIs and short vigilance bouts with short ISIs). In the remaining three cases, we detected a negative relationship. Besides, in 6 of 17 sequences the length of the ISI was associated with the length of the preceding scanning bout ($k = 0$; Table 1), while in the other 11 sequences the ISI was associated with scanning bouts that occurred before or after the ISI ($k > 1$). The coefficients of determination (r) for these correlations varied from 0.41 to 0.64 (mean = 0.52), indicating that the relationship was weak. Non-parametric correlations showed similar relationships between the lengths of ISI and the previous scanning bout. In this case 12 of 40 sequences showed a significant relationship, with concordance coefficients of 0.27–0.68 (mean = 0.33). Ten sequences showed positive and two showed negative associations. Considering parametric and

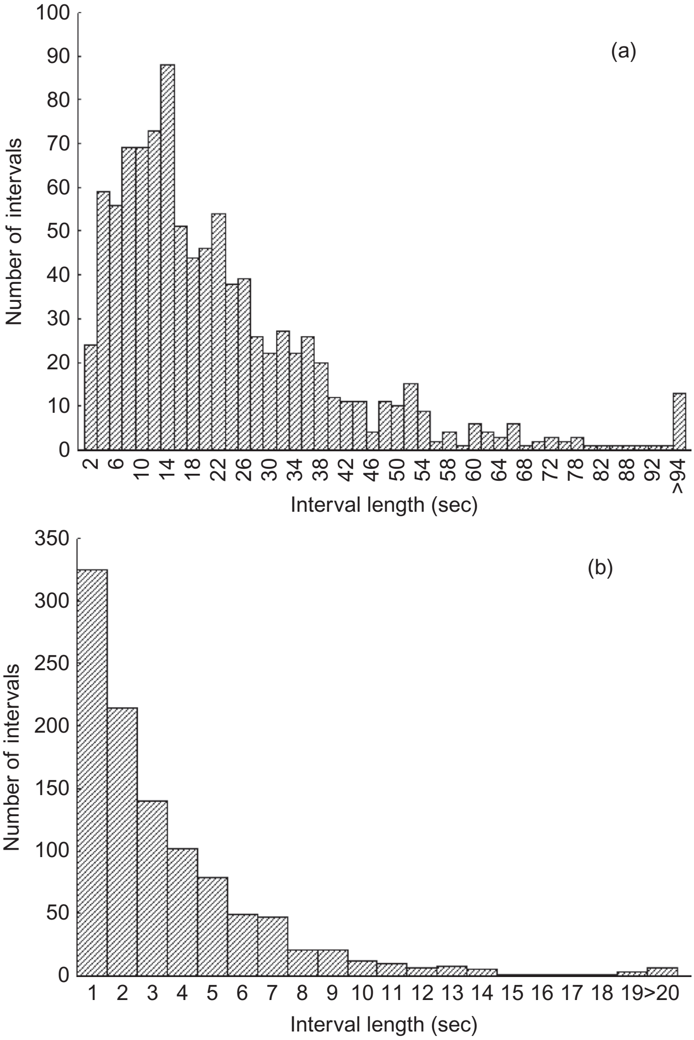

Fig. 1. — Frequency of inter-scan (a) and scan (b) length intervals in seconds obtained from 40 individual behavioural sequences of greater rheas.

non-parametric tests, 9 of 40 series showed consistent temporal SI–ISI dependence. The rearrangement of scanning sequences where we detected dependence of ISIs on previous SIs showed that in 11 of 19 series the probability of obtaining a temporal dependence more extreme than the empirical sequences among ISIs and SIs was lower than 5%. However, in 5 of 11 series we found a temporal dependence of a different order to that observed in the original series in more than 5% of the simulations. Taking into account all parametric tests performed, 36 of 520 showed a significant relationship between SIs and ISIs (6.9% of tests). Although this percentage was higher than for ISI relationships, it is relatively low, and again does not support the presence of consistent regularities in vigilance pattern.

Table 1.
Results obtained from the analysis for independence among inter-scan intervals and between inter-scan and scan intervals of individual behavioural sequences of greater rheas. *k* reveals the lag in the relationship among ISIs and SI.

Individual	Group size	Autocorrelation		Runs test	Cross-correlation		Spearman test	
		P	Coeff. (*k*)	*P*	*P*	Coeff. (*k*)	*P*	Coeff.
42ER♂	1	NS	—	NS	NS	—	NS	—
50ER♂	1	NS	—	NS	NS	—	*0.02*	0.40
94ER♂	1	*0.04*	– 0.44 (5)	NS	*<0.05*	0.40 (– 1)	*0.04*	0.26
86ER♂	1	NS	—	NS	*<0.05*	0.60 (0)	*0.001*	0.38
1ER♂	1	NS	—	*0.05*	NS	—	NS	—
12ER♂	1	*0.03*	0.36 (2)	*0.03*	*<0.05*	0.42 (3)	*0.05*	0.27
30ER♂	1	NS	—	*0.03*	NS	—	NS	—
EGL♂	1	*0.05*	– 0.33 (5)	NS	NS	—	NS	—
FGL♂	1	NS	—	NS	*<0.05*	0.43 (0)	*<0.001*	0.54
LGL♂	1	NS	—	NS	NS	—	NS	—
MGL♂	1	NS	—	NS	*<0.05*	0.44 (3)	NS	—
NGL♂	1	*0.02*	– 0.38 (4)	*0.04*	NS	—	NS	—
QGL♂	1	NS	—	*0.05*	NS	—	NS	—
RGL♂	1	NS	—	*0.008*	NS	—	NS	—
SGL♂	1	NS	—	NS	*<0.05*	– 0.41 (1)	NS	—
69ER♂	10	NS	—	NS	NS	—	NS	—
75ER♂	10	NS	—	NS	NS	—	NS	—
59ER♂	17	*0.02*	0.51 (1)	NS	NS	—	NS	—
15ER♂	2	NS	—	NS	*<0.05*	0.50 (2)	NS	—
AGL♂	2	NS	—	NS	*<0.05*	0.58 (– 5)	NS	—
BGL♂	2	NS	—	NS	NS	—	*0.02*	0.52
DGL♀	2	NS	—	NS	*<0.05*	– 0.63 (– 1)	*0.03*	– 0.27
HGL♂	2	*0.02*	– 0.45 (1)	NS	NS	—	NS	—
OGL♀	2	NS	—	NS	*<0.05*	0.64 (– 1)	*0.01*	0.43
IGL♂	3	*0.04*	0.45 (5)	NS	NS	—	NS	—
JGL♂	3	*0.008*	– 0.49 (4)	NS	*<0.05*	0.58 (– 1)	NS	—
81ER♂	4	NS	—	NS	NS	—	NS	—
CGL♂	4	NS	—	NS	*<0.05*	0.63 (3)	NS	—
GGL♀	4	NS	—	NS	*<0.05*	0.60 (0)	*0.05*	0.41
PGL♀	4	NS	—	NS	*<0.05*	– 0.41 (4)	NS	—
92ER♂	5	NS	—	NS	*<0.05*	0.54 (0)	*0.004*	0.61
KGL♂	5	NS	—	NS	NS	—	NS	—

(*Continued*)

Table 1.

(*Continued*)

Individual	Group size	Autocorrelation		Runs test	Cross-correlation		Spearman test	
		P	Coeff. (*k*)	*P*	*P*	Coeff. (*k*)	*P*	Coeff.
63ER♀	6	NS	—	NS	NS	—	NS	—
2ER♂	6	NS	—	NS	NS	—	NS	—
32ER♂	6	*0.02*	– 0.47 (2)	NS	*<0.05*	0.49 (0)	*<0.001*	0.68
62ER♂	7	NS	—	NS	NS	—	NS	—
93ER♂	7	NS	—	NS	NS	—	NS	—
48ER♂	8	NS	—	NS	*<0.05*	0.55 (0)	NS	—
71ER♀	9	NS	—	NS	NS	—	*0.04*	– 0.23
101ER♂	9	NS	—	*0.04*	NS	—	NS	—

Despite the lack of generality in the vigilance pattern of greater rheas, the presence of regularities in individual sequences could still provide a cue for predators to time their attack. Detection of predictability in the scanning sequence was similar for solitary individuals or individuals in groups (13 of 15 solitary vs 17 of 25 in groups, Fisher-exact test, $P > 0.05$). The probability of detecting temporal dependence in series with parametric tests (auto- and cross-correlations) did not depend on site, group size or sex (logistic regressions, $P > 0.05$ for all analyses). Considering non-parametric tests, the association between ISI and SI was dependent on sex (Δ loglikelihood = 4.13, df = 1, $P = 0.04$), with females showing a significant correlation more frequently than males (5 of 6 females vs 14 of 34 males). However, when we considered the model with sex as the predictive factor for the occurrence of temporal dependence in the series,the correct classification of positive cases (sequences where we detected dependence) was low (33.3%).

Simulations showed that the potential value of predictability of the ISI length for the predator varied with approaching time. Considering $\tau = 15$ sec and 20 sec, predators that use the behavioural sequence of the prey to predict when they should launch the attack had a higher percentage of successful attacks than predators that launch their attacks at the beginning of one randomly selected ISI (Wilcoxon-paired tests, $T = 44$, $n = 25$, $P = 0.02$ for $\tau = 15$ sec; and $T = 18.5$, $n = 23$, $P < 0.001$ for $\tau = 20$ sec; Fig. 2). For shorter approaching times ($\tau = 5$ and 10 sec), we found no differences between predators that monitored the behaviour of preys and those that started their attacks randomly (Wilcoxon-paired tests, $P > 0.05$; Fig. 2).

DISCUSSION

We detected a sequential non-random scanning pattern in 30 of 40 behavioural sequences of greater rheas. Both parametric and non-parametric tests indicated that ISIs departed from randomness and showed temporal dependence from previous ISIs

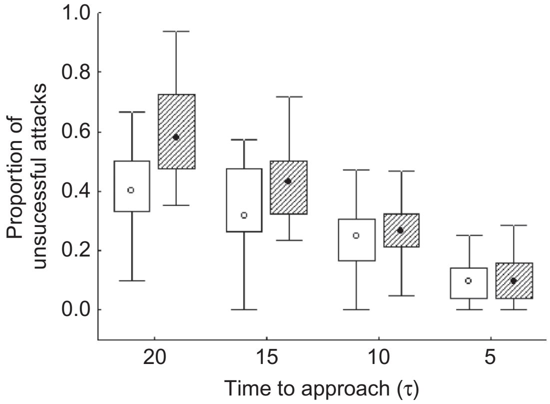

Fig. 2. — Percentage of unsuccessful predator attacks estimated from simple simulations assuming a timing stalking predator that synchronises its attacks with predictable long inattentive periods of the prey (open blocks), and a predator that launches its attacks at the beginning of a randomly selected inattentive period of the prey (dashed blocks). The blocks indicate the results obtained assuming different approaching times of predators (τ). High values of τ represent a predator that takes more time to approach to the minimum distance beyond which the prey is unable to escape. Dots represent median values, boxes are the 25–75 percentiles, and lines represent maximum and minimum values.

and SIs (see Table 1). However, consistency between analyses was low, as only 11 of 40 vigilance sequences showed temporal dependence using parametric and non-parametric tests and re-arranged series. This lack of consistency among analyses does not allow us to reject the hypothesis of sequential randomness in the vigilance pattern of greater rheas. Instead, our data indicate that some individuals showed temporal dependence between ISIs and/or between ISIs and SIs. Potential predators could choose individuals showing such regularities in their vigilance bouts and then synchronise the attack with long ISIs.

The cause of such dependence in the scanning behaviour of individuals is not clear. Previous studies showed that solitary individuals scanned more frequently than individuals in groups, and that males had longer SIs and shorter ISIs than females (REBOREDA & FERNÁNDEZ 1997; FERNÁNDEZ et al. 2003). However, we did not find an effect of group size or sex on the probability of temporal dependence. Previous studies that detected temporal dependence and regularities suggested that such regularities would favour vigilance coordination among individuals in the same group (FERRIÈRE et al. 1996, 1999). This predictability in the sequences would allow individuals to adjust their vigilant bouts with periods of inattention of their companions and the coordination of vigilance would increase the time that the group remained alert, improving the probability of detecting an approaching predator. If this were the case, we would expect that individuals in groups would reveal temporal dependence in their behavioural sequences more frequently than solitary individuals, but this did not happen. Rheas that foraged solitarily and in groups showed a similar probability of temporal correlation. As regards sexual differences, we found that the sequences of males and females had a similar probability of showing temporal dependence, except when we considered the ISI–SI relationship. In this case, females had a higher probability of temporal dependence than males, but correct classification of cases based on this model was low (33%).

If predators use regularities in the vigilance sequence of prey to launch their attacks, prey should avoid such regularities in habitats with high predation risk. Although in our study sites there are no native predators of rheas at present, we consider that the vigilance pattern of individuals still might reflect the relationship between habitat structure and predation risk. Predation risk would be higher in habitats with more vegetation cover, as predators could approach the prey more easily. However, we did not find differences in the probability of detecting temporal dependences between rheas that foraged a bushier, riskier habitat (site 1) and those observed in a more open, less risky habitat (site 2).

Most temporal dependence among ISIs detected on the original series differed from those detected on the randomly re-ordered series. However, we were able to detect temporal dependences among ISIs on re-ordered series of different order than in the original series. We found similar results in correlations between the ISI and the previous SI in re-ordered series. These results did not allow us to discard the possibility that the temporal dependences that we detected are spurious: the consequence of a low number of ISI–SI transitions, or the result of short-term variation in the scanning patterns generated by external stimuli. However, short-term predictability in the vigilance pattern could be still used by predators to launch their attack if they are able to process such short-term vigilance sequences. In particular, the dependence between SI and ISI might be the result of birds applying single scanning rules such as long ISI following long SI and vice versa, and it would be easily used by predators to predict long unattended periods of the prey.

Other studies have also found that scanning sequences of individuals show some degree of predictability (DESPORTES et al. 1989; BEAUCHAMP 2006; BARROS et al. 2008), but these departures from randomness have been interpreted as arising from short-time organisation of animal activities, or the consequence of short-term instability in the series caused by changes in group size, differences in environmental variables, disturbances or any other external stimuli (ROBERTS 1995; RUXTON & ROBERTS 1999; BEAUCHAMP 2006; see also ELGAR 1989). In a recent study, BARROS et al. (2008) showed that black tufted-ear marmosets (*Callithrix penicillata*) altered their vigilance pattern according to specific environmental cues, departing from randomness during exposure to a predator or a novel experimental arena. These animals decreased the ISI length when confronted initially with a predator and later returned to a random pattern of vigilance during subsequent exposures. We obtained behavioural sequences from individuals in stable and apparently undisturbed groups. However, we cannot rule out that undetected stimuli could be responsible for the predictability in the scanning sequences that we observed.

A functional prediction of the sequential predictability hypothesis is that if a predator is able to predict particularly long ISIs of its prey, it could improve its attack efficiency by launching the attack during such intervals (BEDNEKOFF & LIMA 1998). Using simple simulations, we did not find evidence that long prey ISIs would improve the efficiency of an attack. Only when we considered predators that took a long time to approach the prey, or when the approaching speed was low (large τ), was a predator that launched the attack during long ISIs more efficient in its attack than a predator launching an attack at the beginning of a randomly selected inattentive period of the prey.

The value of predictability in the scanning sequence of a prey is dependent on a series of premises, most of them considered improbable or difficult to prove. One of them is that the predator should evaluate long sequences of ISIs and SIs, and estimate accurately the current overall rate of scanning to detect those periodicities (ROBERTS 1996). There is no evidence for such predator capability, and it appears to be rather improbable that predators could do it. Still, a stalking predator using this predictability must time its attack exactly with an adequate period of non-attendance of the prey. Animals usually make time estimation errors when solving laboratory tasks (20–25%; RODRÍGUEZ-GIRONÉS & VASQUEZ 2002), and it is likely that errors would be higher in wild conditions. These timing errors may make launching a synchronised attack even more difficult.

Furthermore, a few studies have shown that predators can process information about prey behaviour. In these studies, predators attacked less vigilant prey individuals or groups (FITZGIBBON 1989; KRAUSE & GODIN 1996; CRESSWELL & QUINN 2004). However, all evidence derived from these studies indicates that predators assess short-term prey behaviour. Instead, the sequential randomness hypothesis assumes that stalking predators would predict and synchronise an attack with a long ISI of the prey. Therefore, prey should avoid producing a predictable, regular vigilance pattern in order to avoid the possibility that the predator will synchronise its attack. In this sense, there is no evidence that predators can process the information derived from the vigilance sequence of prey.

Terrestrial stalking predator behaviour appears to differ from this timing strategy as they appear to approach the prey very slowly, using cover to hide them. This approach requires extensive periods, and does not necessarily involve long-term predictions regarding prey scanning patterns. This approach continues until the predator is located very close to the selected prey (between 50 and 30 m or less, depending on the predator type), when it dashes from the cover towards the targeted prey (e.g. SCHALLER 1972; CURIO 1976; HOPCRAFT et al. 2005; PELLETIER et al. 2006). Considering the stalking strategy that this type of predator apparently uses and the short distance from which predators usually launch their attacks, it is unlikely that they invest time in synchronising their attack with relatively long inattentive periods of the prey. In the southern temperate region, the main native stalking predator of rheas is the cougar. This species launches its attack when it is ≈50 m away from the targeted prey and can run at up to 40–60 km/hr (PELLETIER et al. 2006). Therefore, it would need 3–4 sec to reach its prey. According to our simulations, such a short final approaching interval would not require processing of the vigilance pattern of the prey. Thus, although there is temporal dependence among SIs and ISIs in the scanning behaviour of greater rheas, these regularities would be of little value for a stalking predator. In our studied areas, only feral dogs and humans remain as predators of rheas. Both predators behave rather as opportunistic predators, not caring about the prey behaviour. Dogs usually pursue the prey for long periods until they catch them, whereas humans hunt prey by shooting them, often from a considerable distance.

Concluding remarks

We found temporal dependence among scanning and inter-scanning intervals in behavioural sequences of greater rheas. However, detection of such predictability in the sequences was highly dependent on the statistical analysis we used. Such variation did not allow us to reach a conclusion about the existence of temporal dependence in the vigilance pattern of greater rheas. Dependences involving correlations between ISIs and ISIs and SIs were highly variable, with a high dispersion, and were non-directional, which make them inappropriate for predators to launch their attacks. Therefore, no generalisation about the predictability of scanning sequences in the greater rhea could be derived. The temporal dependence detected could be the result of simple mechanistic rules determined by a compromise between foraging and scanning behaviours. However, although these dependences could be used by a predator to choose an individual prey and to synchronise its attack, we suggest, based on the results obtained from simulations, that they are of little value to a predator.

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