

Interim Report

IR-01-041

Predictability, Chaos and Coordination in Bird Vigilant Behaviour

Régis Ferrière (rferrier@snv.jussieu.fr)
Bernard Cazelles (cazelles@snv.jussieu.fr)
Frank Cézilly (Frank.Cezilly@u-bourgogne.fr)
Jean-Pierre Desportes

Approved by

Ulf Dieckmann
Project Coordinator, Adaptive Dynamics Network

September 2001

About the Authors

Régis Ferrière

Laboratoire d'Ecologie, CNRS UMR 7625, Ecole Normale Supérieure,
46 rue d'Ulm, 75232 Paris cedex 05, France

and

Adaptive Dynamics Network,
International Institute for Applied Systems Analysis
A-2361 Laxenburg, Austria

Bernard Cazelles

UFR de Biologie, Université Paris 7,
2 place Jussieu, 75251 Paris cedex 05, France

Frank Cézilly

Laboratoire d'Ecologie, Université de Bourgogne,
21011 Dijon cedex, France

Jean-Pierre Desportes

Centre National de la Recherche Scientifique,
46320 Sonac, France

Predictability, Chaos and Coordination in Bird Vigilant Behaviour

Régis Ferrière

Bernard Cazelles

Frank Cézilly

Jean-Pierre Desportes

The nature of the scanning dynamics of foraging birds has been debated for more than 15 years (see Bednekoff & Lima 1998 for a review). Previously, we (Ferrière et al. 1996) reanalysed data for five solitary birds (one purple sandpiper *Calidris maritima*, two Barbary doves *Streptopelia risoria* and two choughs *Pyrrhocorax pyrrhocorax*) using nonlinear forecasting, a new statistical approach rooted in the theory of nonlinear dynamical systems. Nonlinear forecasting showed that the vigilant behaviour of the two choughs was dominated by periodicity (with superimposed noise). In contrast, the hypotheses of periodic scanning and pure randomness were rejected for the sandpiper and doves. Further statistical treatments (computation of the Lyapunov spectrum and Kolmogorov entropy) supported the alternative conclusion that the dynamics of scanning in these birds were chaotic. This is important because the high, short-term, and rapidly declining predictability of chaotic scanning may allow birds to coordinate their vigilance at low cost. We developed a mathematical model to probe this hypothesis further. The model revealed that even loose coordination, based on predictions of the neighbour's behaviour only one foraging bout ahead, dramatically reduced individual predictability and enhanced the level of group surveillance, provided that intrinsic, individual vigilance was chaotic.

Ruxton & Roberts (1998) suggest that our (Ferrière et al. 1996) analysis 'does not provide evidence of chaotic patterns in vigilance behaviour', and they question our suggestion that 'chaotic patterns are likely to be adaptive'. Here, we attempt to clarify the points at issue and delineate the areas of agreement and disagreement between Ruxton & Roberts' critique and our original paper. In doing so, we introduce new statistical approaches designed to detect nonstationarity in short sequential data sets.

Ruxton & Roberts (1998) present data on vigilance patterns in terns, and by comparing these data to ours, intend to show that our initial conclusions were erroneous. However, such a comparison is questionable. The correlation coefficient for the tern data reaches only 0.25 for predictions one step ahead. Therefore, noise may account for

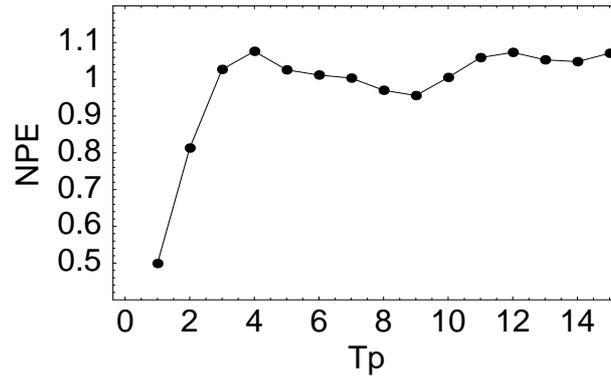


Figure 1. Nonlinear forecasting analysis of the series of scan and interscan obtained from a solitary sandpiper (see Ferrière et al. 1996). Normalized prediction error is plotted against the number of prediction steps.

more than 70% of the variance in terns' scanning, and we can fully agree that the low predictability in Ruxton & Roberts' data 'is not intrinsically generated chaos'. In contrast, correlation coefficients over one step were above 0.80 in all cases we considered (Ferrière et al. 1996), and thus we cannot dismiss our initial conclusions regarding our own data sets. Another issue in this comparison arises from a discrepancy in calculations, revealed by a reciprocal analysis by Drs Ruxton and Roberts and ourselves of some of the dove and tern data sets. The difference in the magnitude of the correlation coefficient may well be an artefact due to the use of different nonlinear forecasting methods. Our original approach was based on Sugihara & May's (1990) method, which is advocated by Wayland et al. (1993). There are several other nonlinear forecasting methods, all of them having many free parameters that must be fine-tuned by the user. Depending on the user's choices, moderate differences may result. One way to avoid discrepancies between different studies of the same data sets is to rely on a 'reference code'. We probed the robustness of our results using a MATLAB program made available by Schiff et al. (1994), which differs from Sugihara & May's algorithm mainly in the statistics used to draw predictability profiles. In the former, predictability statistics is a prediction error, normalized with the prediction error for the mean. An increase of the normalized prediction error with an increased number of prediction steps is the benchmark of chaos. When we applied this method to the sandpiper data (Fig. 1), the results appeared to be consistent with our previous analyses (Ferrière et al. 1996), and our contention that the underlying dynamics of scanning are chaotic.

Ruxton & Roberts (1998) contend that nonstationarity caused by ‘external events’ can explain the pattern they observed, but it is unlikely to explain our results. The data we analysed were of undisturbed birds. The experimental setting of the two doves was rigorously controlled for external perturbations (see Cézilly & Brun 1989), while the three other data sets were of lone birds in natural conditions. One of the data sets previously analysed by Desportes et al. (1989) was suspected of being nonstationary, and therefore was excluded from our analysis. Furthermore, we investigated the effect of putative nonstationarity by comparing predictability portraits from different ‘library/target’ partitions of the data. Our results confirmed the robustness of the predictability portraits in that they did not differ noticeably for different partitions (Ferrière et al. 1996; figures 4a, d, e).

Rigorous statistical tests for nonstationarity are not easy to construct. Statistics based on data partitions ought to take into account the geometrical properties of the data set, and avoid the pitfall of non independence between different parts of the data set (Kennel 1997). Since our initial analysis (Ferrière et al. 1996), new methods have been developed in the context of state-space reconstruction to quantify the degree of nonstationarity of chronological data sets (Kennel 1997). These methods rely on the concept of ‘mutual false nearest neighbours’ (MFNN) in a reconstructed E -dimensional state space (Rulkov et al. 1995) and they naturally account for the geometry and serial correlation of chronological data sets. A simple version suited for relatively small data sets is aimed at computing an MFNN parameter as follows. Suppose that d_1 and d_2 are the average distances to the z nearest neighbours from each point in the first and second half of the data set. Then define d_3 (and d_4) as the average distance of each point in the first and second half, respectively, to the z nearest neighbours that belong to the second (and first) half. The MFNN indices would then be defined as $c_1 = d_2/d_1$, $c_2 = d_3/d_4$ and $c = c_1/c_2$ (Rulkov et al. 1995). Nonstationary series have their c_1 , c_2 and c indices departing from unity. We computed the stationary indices for our longest data set, and compared these with indices from two stationary time series (one chaotic and one noisy-cyclic), and a nonstationary stochastic linear process (Table 1). All series had c values close to 1, but the nonstationary process had much higher c_1 and c_2 values. In the real vigilance data set, all stationary indices were close to 1, supporting our contention that the data we analysed were little affected by nonstationarity.

Table 1. Stationarity indices

Data set	E	z	c_1	c_2	c
Purple sandpiper	2	35	1.097	1.258	0.872
	3	35	1.226	1.126	1.089
Chaotic logistic map (stationary)	2	40	1.026	0.868	1.183
	3	40	0.991	0.908	1.091
Noisy-cyclic logistic map (stationary)	2	40	0.962	0.960	1.002
	3	40	0.925	0.975	0.950
Stochastic linear process with trend (nonstationary)	2	40	2.324	2.279	1.020
	3	40	1.834	1.752	1.047

The stationarity indices were computed by first embedding the chronological series in an E -dimensional state space and choosing a time lag τ (equal to one here) (see Sugihara & May 1990). We applied the mutual false nearest neighbours method (see text for details) to the longest data set we had available (252 scan and interscan durations from a solitary purple sandpiper). For purpose of comparison, we generated 500 points from a chaotic logistic map ($x_{t+1} = 3.95 x_t (1-x_t)$), from a noisy-cyclic logistic map ($x_{t+1} = 3.5 x_t (1-x_t) + u_t$, where u_t is drawn uniformly from $(-0.2, +0.2)$) from a nonstationary stochastic linear process ($x_t = 0.02 t + b_t$ with b_t drawn uniformly from $(-20, +20)$).

Ruxton & Roberts' (1998) discussion of nonstationarity implies that any kind of external stimuli results in nonstationary scanning dynamics. External perturbations, however, like additive, uncorrelated noise, do not cause a stationary time series to become nonstationary (e. g. Tong 1990). Furthermore, in all data sets that we identified as chaotic (Ferrière et al. 1996), 'unpredictable external stimuli' that would have been 'detected by the birds, but not the investigators' (quotes from Ruxton & Roberts 1998) could account for at most 20% of the variance in vigilance dynamics. Food handling may or may not generate nonstationarity. As foraging proceeds, the selection of food items with differing characteristics may lead to a smooth change in handling time. For example, a bird always selecting the smallest seeds available will eventually handle larger and larger seeds, causing lower scanning rates, and possibly, nonstationarity. If handling time varies randomly, however, stationarity should be preserved.

The arrival or departure of a bird to a group may also perturb the scanning dynamics of an individual in that group, and nonstationarity may result from abrupt changes in group size (Roberts 1995). We hypothesize that, as the group size changes, changes in the scanning regime may correspond to jumps between different attractors. To probe this prediction, one can seek 'slices' in the chronological series that would belong to the different attractors, by using the stationary indices introduced above. We operated this approach on a simulated data set comprising three different bouts, generated by three dynamical systems (chaotic logistic map, Henon map and noisy-cyclic logistic map, Fig.

2a). Although each bout was generated by a stationary process, the series as a whole was nonstationary ($c_1 = 1.286$, $c_2 = 2.095$ and $c = 0.614$ with $E = 3$ and $z = 100$). We detected the three bouts by computing the d_i 's (involved in stationary indices) for a fixed and a mobile time window (instead of the first and second halves of the series). Initially the windows span the first and second halves of the first bout. The corresponding indices reflect the stationarity of that first bout (Fig. 2b, c). As the mobile window enters the second bout, the stationarity indices move away from 1, indicating that the first and the second bouts correspond to different attractors. As the mobile window enters the third bout, the stationarity indices undergo substantial changes again; c drops to near 1 while c_1 reaches a much lower value that shows unambiguously that a third attractor, different from the other previous two, has been attained. This method could be applied to series of behavioural data of sufficient length to identify qualitative changes in behaviour in response to external stimuli, uncontrolled or undetected by the investigators. Ruxton & Roberts' (1998; figure 2) data suggest to us that the arrival of other birds to the group trigger transitory oscillations in scanning, and that once these transients are dissipated, scanning returns to the same preperturbation regime. The statistical procedure outlined above could be used to assess this interpretation.

Ruxton & Roberts question our hypothesis that chaotic vigilance is adaptive in birds that coordinate their vigilance. Our argument about coordination was based on the idea that depending on whether intrinsic, individual vigilance is random, periodic or chaotic, coordination may have different influences on effective, individual vigilance patterns (and on group vigilance as well). This is why we analysed data collected from solitary birds. The next step should be to investigate how the predictability profiles of lone birds are affected when these birds are foraging in a group.

The mathematical model we developed to assess the effect of coordination on vigilance predictability demonstrated that coordination had a considerable effect on individual predictability: the high, short-term predictability of chaotically scanning birds dropped dramatically when they coordinated vigilance (Ferrière et al. 1996, figure 6c). For example, the predictability of the next interscan duration, as measured by a correlation coefficient, is 0.99 when the birds scanned independently, whereas it dropped to 0.25 when individuals coordinated vigilance. Considering two interscans ahead, predictability scores 0.10 with coordination versus 0.98 without; thus, in a group comprised of coordinating and noncoordinating birds that scan chaotically, the coordinators eventually assume a significant reduction in individual predictability compared with noncoordinators, thereby making noncoordinators more vulnerable to predation. If predators time their attack on very short-term predictions only, the selective pressure favouring coordinators should be higher. The nature of the environment that a predator crosses during the final stage of its attack will determine whether predictions on a medium term influence the success of the attack.

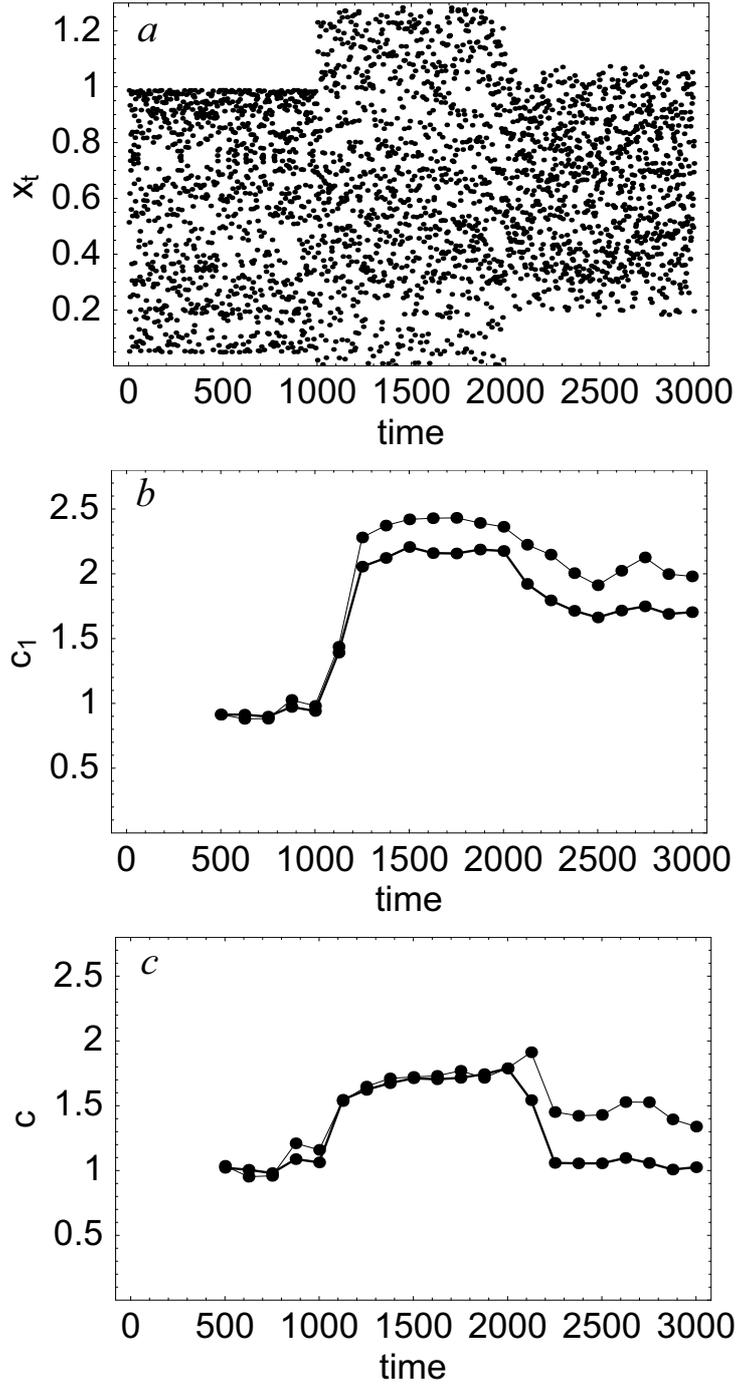


Figure 2. Identifying different attractors in nonstationary data sets. (a) A nonstationary time series consisting of three bouts generated by different dynamical systems: a chaotic logistic map, the Henon map (taking the absolute value of $x_{t+1} = 1 - 1.4 x_t^2 + y_t$ and $y_{t+1} = 0.3 x_t$) and a noisy-cyclic logistic map (see Table 1 for the models' equations). (b) Stationary index c_1 . (c) Stationary index c . Thin line: $E = 2$; Bold line: $E = 3$, where E is the the embedding dimension of the reconstructed phase space (see Table 1, text, and Sugihara & May 1990 for details). Stationary indices are computed by making use of a fixed and a moving window, each equal in width to 250 time units. The fixed window spans the first 250 data points in the first bout. The moving window is initially located over $t = 251-500$. The abscissa in (b) and (c) indicates the right end of that window as it is moved forward along the data set. Wide fluctuations in stationary indices occur as the moving window enters a data bout that corresponds to a different attractor.

Our model did not involve costly mechanisms for birds to monitor their neighbours, nor did it presuppose outstanding capability of the birds to fine-tune scanning rates. We only assumed loose coordination, involving predictions one step ahead only. Also, birds could apply only crude corrections to their intrinsic pattern of vigilance. Furthermore, coordination is not blind self-sacrifice, but a conditional strategy that relies on the ability to ‘cooperate’ or ‘defect’, depending on the partners’ (neighbours’) behaviour. The means by which coordination is stable against cheaters vary, based on repeated interactions between sessile organisms, or discrimination in a highly mixed population (see Ferrière & Michod 1996; Ferrière 1998). This is consistent with Gaston’s (1977) and Inglis & Lazarus’ (1981) hypotheses that coordinated scanning may hold in groups with quasi-permanent membership or in large flocks of mobile individuals (also see Elcavage & Caraco 1983).

Empirical evidence for coordination remains scarce, possibly because coordination really is rare. If the putative costs of coordination are buffered when individual vigilance is chaotic, then the puzzle of understanding the scarcity of coordination in group vigilance is even more challenging. Previous statistical analyses have looked for coordination as expressed by a larger probability of a bird putting its head down when its companions have their heads up. Our model presents a more subtle organization of corporate vigilance which may require more sophisticated statistical procedures to be detected. For example, standard linear cross-correlation may fail when applied to systems involving nonlinear correlations like those in our model, whereas nonlinear forecasting opens a promising avenue to investigate dynamical interdependence among these non-linear systems (Schiff et al. 1994).

We must reiterate our original conclusion (Ferriere et al. 1996), that vigilance may or may not be chaotic, depending possibly on the species, the individual and the environmental conditions. Although there is no inferring unambiguously the chaotic nature of dynamical processes from declining profiles of predictability (e.g. Cazes & Ferriere 1992), the nonlinear forecasting method we used stands among the most robust methods currently available to detect chaos in short data sets (Schreiber & Schmitz 1997), and the geometry of sequences of scanning times conform to a favourable case where nonlinear analysis is more efficient (e.g. Geest et al. 1993). Why vigilance is driven by deterministic chaos in some cases, but involves more regular periodicity in others, can only be answered by carefully designed experiments. On the theoretical side, vigilance continues to raise challenging problems, including the development of new statistical procedures for seeking coordination in real data, and the construction of individually-based models to assess the evolutionary stability of coordination.

References

- Bednekoff, P. A. & Lima, S. L. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology and Evolution*, 13, 284-287.
- Cazelles, B. & Ferriere, R. 1992. How predictable is chaos? *Nature*, 355, 25-26.
- Cézilly, F. & Brun, B. 1989. Surveillance et picorage chez la tourterelle rieuse: effets de la présence d'un congénère et de la dispersion des graines. *Behaviour*, 110, 146-160.
- Desportes, J.-P., Metcalfe, N. B., Cézilly, F., Lauvergeon, G. & Kervella, C. 1989. Tests of the sequential randomness of vigilant behaviour using spectral analysis. *Animal Behaviour*, 38, 771-777.
- Elcavage, P. & Caraco, T. 1983. Vigilance behaviour in house sparrow flocks. *Animal Behaviour*, 31, 303-304.
- Ferriere, R. 1998. Help and you shall be helped. *Nature*, 393, 517-519..
- Ferriere, R. & Michod, R. E. 1996. The evolution of cooperation in spatially heterogeneous populations. *The American Naturalist*, 147, 692-717.
- Ferriere, R., Cazelles, B., Cézilly, F. & Desportes, J.-P. 1996. Predictability and chaos in bird vigilant behaviour. *Animal Behaviour*, 52, 457-472.
- Gaston, A. J. 1977. Social behaviour within groups of jungle babblers (*Turdoides straitus*). *Animal Behaviour*, 25, 828-848.
- Geest, T., Olsen, L. F., Steinmetz, C. G., Larter, R. & Schaffer, W. M. 1993. Nonlinear analyses of periodic and chaotic time series from the peroxydase-oxydase reaction. *Journal of physical Chemistry*, 97, 8431-8441.
- Inglis, I. R. & Lazarus, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Zeitung die Tierpsychologie*, 57, 193-200.
- Kennel, M. B. 1997. Statistical test for dynamical nonstationarity in observed time-series data. *Physical Review E*, 56, 316-321.
- Roberts, G. 1995. A real-time response of vigilance behaviour to changes in group size. *Animal Behaviour*, 50, 1371-1374.
- Rulkov, N. F., Sushchik, M. M., Tsimring, L. S. & Abarbanel, H. D. I. 1995. Generalized synchronization of chaos in directionally couples chaotic systems. *Physical Review E*, 51, 980-994.
- Ruxton, G. D. & Roberts, G. In press. Are vigilance sequences a consequence of intrinsic chaos or external changes? *Animal Behaviour*.

- Schiff, S. T., Sauer, T. & Chang T. 1994. Discriminating deterministic versus stochastic dynamics: Dynamics in neuronal activity. *Integrative Physiology and Behaviour Sciences*, 29, 246-261.
- Schreiber, T. & Schmitz, A. 1997. Discrimination power of measures for nonlinearity in a time series. *Physical Review E*, 55, 5443-5448.
- Sugihara, G. & May, R. M. 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. *Nature*, London, 344, 734-741.
- Tong, H. 1990. *Non-linear Time Series: A Dynamical System Approach*. Oxford: Oxford University Press.
- Wayland R., Pickett D., Bromley D. & Passamante, A. 1993. Measuring the predictability of noisy recurrent time series. *International Journal of Bifurcation and Chaos*, 3, 797-802.