

## Alertness signalling in two rail species

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Predators and prey benefit if predators can assess the difficulty of prey capture by obtaining information about the level of alertness of potential prey. Alertness can be inferred indirectly, for example, from the prey's body posture. However, we should expect prey to inform the predator of their state of awareness if they would benefit from curtailed pursuit (Woodland et al. 1980; Tilson & Norton 1981; Bildstein 1983; Caro 1986; Hasson et al. 1989).

The moorhen, *Gallinula chloropus*, and purple gallinule, *Porphyrio porphyrio*, show a strongly contrasting rump patch, constantly flashed by rapidly jerking the tail up and down (tail-flicking). The fact that the rate of tail-flicking increases with increasing risk of predation in both species (Woodland et al. 1980; Alvarez 1989) suggests that this behaviour may function as an alarm signal. The fact that solitary individuals are often observed tail-flicking suggests that the behaviour plays a role in prey–predator communication, rather than acting as an intraspecific warning signal (Alvarez 1989).

I tested whether the function of rump patch flashing in both rail species is better explained as an intraspecific warning signal or as communication of alertness towards predators. According to the second hypothesis we should expect tail-flicking to be oriented towards the direction from which predators are more likely to come; and rate should be positively correlated with individual vigilance.

I observed adult birds on a 16-km length of the banks of the Guadaira River, near the Guadalquivir marshes from October 1991 to January 1992. The birds were searching for food while walking on the mud shores. Along the river banks cover was provided by a continuous belt of cattail, *Typha domingensis*. I video-taped the birds from a car, following a dirt road along the opposite river bank, and stopping about 100 m from them. I counted up to 51 moorhens and 28 purple gallinules per day.

I recorded each upward movement of the tail as an instance of tail-flicking. During vigilance bouts,

the bird stopped its activity for a variable period of time and remained motionless with the neck straight up. Vigilance was measured as the rate of looking up/min. There was no postural constraint on tail-flicking.

The predators were several marsh harriers, *Circus aeruginosus*, which frequented the zone, foraging by flying low (about 5–10 m) along the shore. Both rail species reacted to a flying marsh harrier by moving at variable speed towards cover.

In a series of observations (moorhens: 19; purple gallinules: 16), rails foraging alone were video-taped (camera with 500 mm lens) when a marsh harrier was seen flying in their general direction at least 200 m away, until the rail concealed itself in the cattail thicket. A second observer observed the harrier through 10 × 40 binoculars, to make sure that it moved in the subject's general direction.

From the video tapes I compared the number of tail-flicks shown by each subject from the moment it started to move towards cover until it disappeared within the cattail thicket with that shown by the same subject during a period of the same length immediately preceding escape. Only periods lasting at least 20 s before and 20 s after flight started were considered.

In another set of 31 observations, in the absence of predators, I arbitrarily chose a moorhen on the periphery of a group (group size: 5–11). I recorded its rate of tail-flicking when its rump patch was oriented away or towards the group, that is, when no group partner could see or when some of them were able to see the subject's rump patch. This procedure could not be applied to purple gallinules, as they usually foraged solitarily.

In a third set of observations (moorhens: 16; purple gallinules: 30), also in the absence of predators, I recorded the tail-flicking rate of subjects foraging solitarily, with no conspecific in view and not further than 1 m from cover, when the rump patch faced either towards or away from cover.

Table I. Median and interquartile range of observed rates of tail-flicking (in flicks/min)

	Moorhen		Purple gallinule	
	Median	Interquartile range	Median	Interquartile range
<b>Marsh harrier present*</b>				
Before moving to cover	16.80	32.55	22.34	25.55
After moving to cover	42.86	27.76	50.12	9.89
<b>Marsh harrier absent</b>				
Distance to cover†				
Near cover	6.00	21.18	24.27	23.27
Far from cover	12.86	28.32	34.88	20.67
Rump patch orientation‡				
Towards cover	10.63	18.75	39.56	35.94
Away from cover	15.79	28.76	61.21	47.42

\*Moorhen:  $T=13$ ,  $N=19$ ,  $P<0.01$ . Purple gallinule:  $T=7.5$ ,  $N=16$ ,  $P<0.01$ , Wilcoxon test.

†Moorhen:  $T=2$ ,  $N=10$ ,  $P<0.01$ , Wilcoxon test. Purple gallinule:  $z=0.90$ ,  $N=44$ ,  $N=46$ ,  $P>0.05$ , Mann-Whitney  $U$  test.

‡Moorhen:  $T=71$ ,  $N=16$ ,  $P>0.05$ . Purple gallinule:  $z=2.97$ ,  $N=30$ ,  $P<0.01$ , Wilcoxon test.

In a fourth set of observations (moorhens: 70; purple gallinules: 89), also in the absence of predators, I chose subjects arbitrarily and observed them through a telescope for no more than 5 min or until they disappeared from view. I recorded group size (birds within visual contact and a maximum nearest neighbour distance of 30 m between group members), whether the focal subject was nearer or further than 1 m from the edge of the cattail thicket, vigilance and number of tail-flicks.

In both rail species the rate of tail-flicking significantly increased when, after detecting a marsh harrier flying towards them, the birds started to move towards cover (Table I).

Moorhens feeding on the periphery of a group tail-flicked away from the group at a faster rate than towards the group (away from group: median = 17.50, interquartile range = 10.47 flicks/min,  $N=31$ ; towards group: 5.60, 15.65 flicks/min,  $N=31$ ;  $z=2.03$ ,  $N=31$ ,  $P<0.05$ , Wilcoxon test).

Among birds feeding solitarily near cover, only for the purple gallinule was the rate of tail-flicking significantly higher when flicking away from cover (in the direction from which harriers could come) than when doing so towards cover (from which harriers could not come, Table I).

Both rail species' tail-flicking rate showed a positive relationship with individual vigilance (moorhen:  $r_s=0.58$ ,  $N=70$ ,  $P<0.01$ ; purple gallinule:  $r_s=0.59$ ,  $N=89$ ,  $P<0.01$ , Spearman rank correlation, Fig. 1). For the group-feeding moorhen,

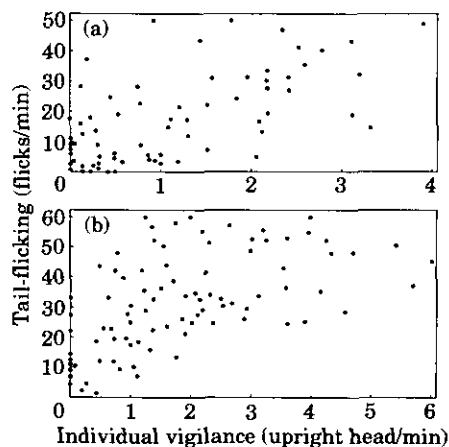


Figure 1. Rate of tail-flicking versus rate of individual vigilance in (a) moorhens and (b) purple gallinules.

group size was negatively correlated with tail-flicking ( $r_s=-0.39$ ,  $N=70$ ,  $P<0.05$ ) and with individual vigilance ( $r_s=-0.31$ ,  $N=70$ ,  $P<0.05$ ).

When the mean tail-flicking rates of moorhens near cover (51 observations) for each group size (1–10) were matched-paired with the rates for the same group sizes and far from cover (40 observations), those animals foraging far from cover flicked at a faster rate. Solitary foraging purple gallinules showed no significant difference (Table I).

The results suggest that tail-flicking in both rail species is directed towards predators rather than

towards conspecifics: its rate increased (1) when a predator was present, (2) when subjects ventured far from cover, (3) when oriented away from conspecifics, and (4) towards the direction from which aerial predators were more likely to come. There was also a positive correlation with individual vigilance and a negative one with group size.

When a predator is present, rapid tail-flicking probably indicates that the bird has detected it. As a consequence, foraging predators probably avoid wasting time by not starting the hunt, and the prey are spared unnecessary chases. Similar conclusions on honest communication of alertness towards predators as a way to deter attack were also reached by Woodland et al. (1980) for the eastern swamphen, *P. porphyrio*, and by Tilson & Norton (1981) for the klipspringer, *Oreotragus oreotragus*.

When predators are not in view, rails may anticipate their presence and inform them about their state of awareness. Although high tail-flicking rates when far from cover can be explained as a consequence of high levels of vigilance when in risky situations, it could be that when less visible (closer to cover) it is less useful to send any visual signal.

The simplest way to explain how honest signaling of vigilance by tail-flicking could arise would be through the need of vigilant birds (or of an individual during periods of high vigilance) not to waste too much time escaping. In this case information about their state of awareness (tail-flicking) would be of mutual benefit to the predator and the signaller. On the other hand, it would not be worth

non-vigilant birds (or an individual during periods of no vigilance) increasing their already higher vulnerability and attracting extra predators by tail-flicking.

Although information on individual variation in vigilance ability is not available, vigilant individuals could avoid wasting energy by tail-flicking only at appropriate times, whereas non-vigilant birds might find the energetic costs of tail-flicking prohibitive since they would be poor judges of when it is safe to turn off the signal.

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