

## Female Baboons' Responses to Male Loud Calls

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### Abstract

Male baboons (*Papio cynocephalus ursinus*) give loud, two-syllable 'wahoo' calls in response to predators (*alarm* wahoos) and during aggressive displays that may include multiple males chasing each other or females (*contest* wahoos). Although acoustic analysis has revealed significant differences between the two calls, these differences are subtle and the two subtypes can be difficult for humans to distinguish. Whatever the evolutionary mechanisms that might have acted on the production of acoustically graded loud calls, it would seem to be adaptive for listeners to discriminate among calls that are given in qualitatively different contexts. This is particularly true in the case of female baboons. *Alarm* wahoos, which are given during predator encounters, demand qualitatively different responses from *contest* wahoos, which are given in contexts when females are at risk of harassment and infanticide by males. In playback experiments, females responded for significantly longer durations to *alarm* than to *contest* wahoos. Moreover, only *alarm* wahoos caused females to flee. Despite their acoustic similarity, female baboons appear to associate *alarm* and *contest* wahoos with qualitatively different events.

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### Introduction

Theory suggests that loud calls transmitted over long distances should be unambiguously distinct, particularly when they serve markedly different functions and supporting contextual and visual cues are absent (Marler 1965, 1967, 1976; Gautier & Gautier-Hion 1977, 1988). However, many non-human primate species, including some that inhabit forests, produce acoustically similar loud calls in qualitatively different contexts (e.g. the alarm and territorial calls of male diana monkeys, *Cercopithecus diana*: Zuberbuhler et al. 1997, 1999; the alarm and territorial calls of langurs, *Presbytis* spp: Hohmann & Vogl 1991; Steenbeek et al. 1999; the alarm calls of Barbary macaque, *Macaca sylvanus*: Fischer 1998,

Fischer & Hammerschmidt 2001; and the alarm and contact barks of female baboons, *Papio cynocephalus ursinus*: Fischer et al. 2001a,b). Although acoustical analysis often reveals significant differences among calls produced in different contexts, these differences are frequently subtle, making call subtypes difficult for humans to distinguish, particularly over long distances.

Male baboons in the Okavango Delta of Botswana give two acoustically graded loud calls, termed 'wahoos', in a variety of different contexts: (1) as alarm calls to leopards or lions (*alarm* wahoos), (2) when a male is separated from the group and appears to be disoriented or lost (*contact* wahoos), (3) during inter-group encounters, when a male may herd females or chase other males, (4) during within-group interactions, again accompanied by aggression or displays that include running and leaping through the trees, and (5) at or before dawn, in single- or multi-male calling bouts, typically in the absence of aggression. Wahoos given during the last three contexts are acoustically similar to one another and are collectively termed *contest* wahoos (Fischer et al. 2002; Kitchen et al. 2003).

Despite their superficial similarity, acoustic analysis has shown that *alarm* and *contest* wahoos are significantly different from each other (Fischer et al. 2002). *Contest* wahoos are usually given at a higher rate, exhibit lower frequency characteristics, have a longer 'hoo' duration, and a relatively louder 'hoo' portion than *alarm* wahoos. Both *alarm* and *contest* wahoos also exhibit significant differences among individuals, which potentially allows listeners to identify who is calling. *Contact* wahoos are acoustically similar to *contest* wahoos, but given at a much lower rate.

Whatever the evolutionary mechanisms that might have acted on the production of acoustically graded loud calls, it would seem to be adaptive for listeners to discriminate among calls that are given in qualitatively different contexts. This is particularly true for female discrimination of male wahoos. *Contest* wahoos typically occur during aggressive interactions among males, when females and their infants are at considerable risk of attack. During the study described below, females were chased or physically attacked in 67% of 354 aggressive interactions initiated among males. Aggressive displays by males also occasionally result in infanticide, the most common cause of infant mortality in Okavango baboons (Palombit et al. 2000; Cheney & Seyfarth unpubl. data). Females frequently flee from male aggression and hide in dense bush, apparently to avoid notice. In contrast, when predators are encountered, females often escape onto the terminal branches of trees, where they are very conspicuous. Predation is suspected to account for almost all adult and juvenile mortality in this population (Bulger & Hamilton 1987); annual mortality among females averages 9% ( $n = 10$  yr). Because females respond to male-male aggression and predators in qualitatively different ways, it would seem advantageous for them to distinguish between *alarm* and *contest* wahoos.

In many primate species, listeners discriminate among subtypes of acoustically graded loud calls. For example, listeners respond differently to 'typical' variants of female baboons' *contact* and *alarm* barks, although they apparently fail to discriminate intermediate forms (Fischer et al. 2001b). Similarly, Barbary

macaques reliably discriminate between categories of shrill alarm barks (Fischer 1998; Fischer & Hammerschmidt 2001), and female diana monkeys distinguish male eagle alarm calls from acoustically similar leopard alarm calls (Zuberbühler et al. 1997, 1999).

Here we describe a series of playback experiments designed to test whether female baboons discriminate between the *alarm* and *contest* wahoos given by males. By conducting playback experiments in roughly the same behavioural and ecological contexts, and by controlling both the rate and number of calls produced, we hoped to determine whether acoustic properties alone allow listeners to distinguish between a predator encounter and male aggression.

## Methods

### Study Site and Population

Playback experiments were conducted in the Moremi Game Reserve, Botswana, between February 2000 and March 2001. Grasslands in this region flood annually, leaving elevated 'islands' edged with forest exposed. Islands can be less than one to hundreds of hectares in size (Hamilton et al. 1976; Ross 1987). During floods, baboons continue to ford the submerged plains and move between islands throughout their range.

The main study group, C, has been observed since 1977. All individuals are easily identifiable and the matrilineal relatedness of all natal animals is known. Subjects are fully habituated to observers on foot. During this study, C group contained 78–88 animals, including 22–25 adult females. The mean number of adult males on any given day was 12. The number of males fluctuated due to immigrations, emigrations, maturation and death.

### Stimulus Selection and Construction

Wahoo vocalizations were recorded during male–male contests and predator encounters using a Sennheiser ME80 directional microphone (Wennebostel, Germany) and a Sony PCM-M1 digital tape-recorder (Tokyo, Japan). Only calls that had been recorded in unambiguous contexts were selected as stimuli for playback experiments. Almost all *alarm* wahoos were recorded during encounters with clearly visible lions. The one exception was an alarm bout produced while the group demonstrated typical predator avoidance behaviour and several members looked fixedly at one location while alarm-calling. Although we were unable to see the predator, subsequent investigation revealed fresh lion tracks.

Previous acoustic analysis revealed a number of parameters that distinguish *alarm* from *contest* wahoos (Fischer et al. 2002). However, these parameters grade along a continuum and calls from both contextual categories can overlap according to more than one acoustic feature. Recordings were therefore subjected to acoustic analysis prior to playback. We selected as stimuli only those calls whose spectral properties and the context in which they were recorded unambiguously assigned

them to either the *alarm* or *contest* category. Acoustic properties of a typical *alarm* wahoo included a relatively quiet and short 'hoo' component ( $< 100$  ms) and a 'wa' component with a mean peak frequency of 0.79 kHz and a mean peak frequency at onset of 0.65 kHz, whereas typical *contest* wahoos had longer, relatively louder 'hoo' components ( $> 100$  ms) and lower frequencies in the 'wa' component (overall peak: mean = 0.72 kHz; peak at onset: mean = 0.48 kHz).

We had originally hoped to also investigate the subjects' responses to intermediate forms of each wahoo subtype (see Fischer et al. 2001b). Unusually heavy rainfall and flooding, however, prevented the use of a vehicle for much of this study. As a result, playback equipment (see below) often had to be carried or poled by canoe over floodplains. This constrained our ability to conduct trials.

Although *contest* wahoos were relatively easy to record, we were limited by the number of recordings we obtained in the *alarm* context. Suitable recordings of wahoos in both contexts were eventually acquired from six resident males. One male served as the signaller in four paired trials, one in three, one in two, and three in one. One male was killed by a lion before his calls could be used more than once, and two other males emigrated from the group before their calls could be used multiple times.

Using software for waveform analysis (Cool Edit 2000, Synttrillium Software, Phoenix, Arizona, USA), we constructed two paired sequences of each male's calls, each containing either three *alarm* or three *contest* wahoos. Each call in the series was separated by 3 s of silence, with the average duration of each sequence lasting 11 s. The rate and number of calls in the sequence, therefore, provided no information about its acoustic subtype. In creating playback sequences, we attempted to use three different calls from the same male. In the case of one male's *alarm* wahoo sequence, however, we were forced to repeat the same call three times. One other male's *contest* wahoo sequence consisted of two calls, with one exemplar appearing as the first and third call in the series.

Baboon wahoos are loud vocalizations, audible for at least 1 km and with typical mean amplitudes of over 90 dB at 5 m. Because they are also relatively low frequency calls, with their strongest energy concentrated between 0.25 and 2 kHz (Fischer et al. 2002), they require a large loudspeaker and considerable amplification for playback. In these experiments, we used an Electro-Voice SX-2000 loudspeaker (Burnsville, Minnesota, USA,  $82 \times 66 \times 43$  cm) powered by a Pioneer GM-X922 amplifier (Tokyo, Japan). To ensure that amplitude remained constant within and between sequences and was similar to sound levels during natural wahoo production (mean = 92 dB at 5 m;  $n = 14$ ), we calibrated recordings in the field using a Realistic sound level meter (RadioShack, Fortworth, Texas, USA, referenced at 20 uPa, accurate at  $\pm 2$  dB at 114 dB). Playback recordings had a mean amplitude of 93 dB (range = 89–95 dB) at 5 m from the playback source and a mean amplitude of 62 dB (range = 60–66 dB) at 75 m through vegetation, which simulated experimental conditions.

Subjects were 12 lactating females. By focusing on females who were vulnerable to infanticide, we hoped to maximize the potential for a strong reaction to the sound of a *contest* wahoo. During the period that the playbacks

were conducted, however, there were no recent dominant male immigrants in the group, with the result that females heard only the wahoos of males who were unlikely to be infanticidal (Palombit et al. 2000). This may have affected the strength of their responses to *contest* wahoos.

### Experimental Protocol

All playbacks were conducted following a period of at least 1 h when no wahoos of any type had been heard, no predators or other baboon groups had been sighted, and no male–male aggression had occurred. For approximately the last half of this period prior to playback, one observer located and followed the focal female to ensure that she was not involved in aggressive interactions with any group members or encountered any predators.

Trials were conducted in wooded habitats with low visibility, at boundary or overlap areas of the group's range. Such locations ensured that playbacks occurred in areas of increased predation risk, where the group had previously interacted with neighbouring groups and where the potential for encountering a new immigrant male was relatively high.

Prior to playback, a second observer set up the speaker at a mean distance of 74.8 m from the subject (range 60–91 m). The speaker was placed in the same relative direction from the subject as was the male whose calls were to be played. A third observer remained with this male to verify his location and to ensure that he was not close to the subject when the call was broadcast. Because the group was often dispersed over distances as great as 500 m, these conditions were easily met. On average, the signalling male was 166 m (range = 81–300 m) from the speaker at the time of the broadcast. All observers were in contact via two-way radios, so that trials could be aborted if the female moved, oriented in the direction of the speaker, or became involved in a social interaction.

Playbacks were conducted only when subjects were feeding or sitting with their heads oriented downward and away from the speaker, at least 2 m from all other individuals except dependent offspring. Subjects were filmed for 15 s prior to playback and 1 min afterwards. Below, we restrict our analysis to the 15 s following the onset of each call sequence. The results remain the same, however, if the longer period is considered.

The order of presentation of *contest* and *alarm* wahoos for each subject was randomly determined. All playbacks were separated by at least 4 d. Trials involving the same female subject or the same male signaller were separated by at least 1 wk.

Following each trial, a 45-min focal animal sample (Altmann 1974) was conducted on the subject, and observers remained with the group for at least 1 h.

### Data Analysis

We predicted that the subject would respond to playback sequences both by orienting towards the concealed speaker and by scanning the area around them.

We therefore scored six categories of responses: (1) latency to orient towards the speaker, (2) latency to begin scanning in any direction, (3) duration of looking towards the speaker, (4) duration of scanning, (5) latency to move at least 3 m (this distance was chosen to exclude movements associated with feeding), and (6) the duration of moving. All latency measures were calculated from onset of the first wahoo in a sequence. We calculated duration measures by subtracting the amount of time spent looking toward the speaker or scanning the area in the 15 s prior to playback from the total amount in the 15 s after recording onset. We also noted the behaviour and location of the subject's dependent offspring, as well as the occurrence of any *alarm* or *contest* wahoos during or within the hour following the trial.

## Results

### Subjects' Responses

During approximately 2880 h of observation, male *alarm* wahoos were heard at an average rate of once every 48 h. However, males also produced *alarm* wahoos at night, when leopard attacks are most common; so approximations derived from day-time observations underestimate actual rates. Male *contest* wahoos were produced at an average rate of once every 11.3 h of observation. Again, however, these rates are underestimates, as males also gave *contest* wahoos during pre-dawn choruses.

Although we did not gather systematic data on females' responses to naturally occurring wahoos, our observations suggested that females typically responded to *contest* wahoos less strongly than to *alarm* wahoos. Indeed, they often appeared to ignore or to orient only briefly to short bouts of *contest* wahoos and only became vigilant or fled if calling rates escalated, calling was nearby, or calling was accompanied by visible aggression. Conversely, *alarm* wahoos evoked stronger responses, particularly if calling persisted or if one signaller was joined by others. In such circumstances, females usually startled, oriented towards the signaller, and often ran toward or into trees.

In playback experiments, the initial response of focal subjects, particularly upon hearing *alarm* wahoos, was often a body shudder or 'startle,' a cessation in chewing, and an immediate sharp snap up of the head. Most subjects immediately oriented towards the speaker (during seven of 12 *contest* and 10 of 12 *alarm* trials) and then rapidly scanned the area around them. Two subjects immediately scanned the area opposite the speaker first, and then oriented towards the speaker (during one *contest* and one *alarm* trial). Two other subjects looked opposite the speaker briefly before resuming feeding (both during *contest* trials). Finally, three subjects never looked up during two *contest* and one *alarm* trial.

Overall, females responded more strongly to *alarm* wahoos than to *contest* wahoos. Subjects' latency to orient in the direction of the speaker was shorter following playback of *alarm* wahoos than *contest* wahoos (Fig. 1; two-tailed

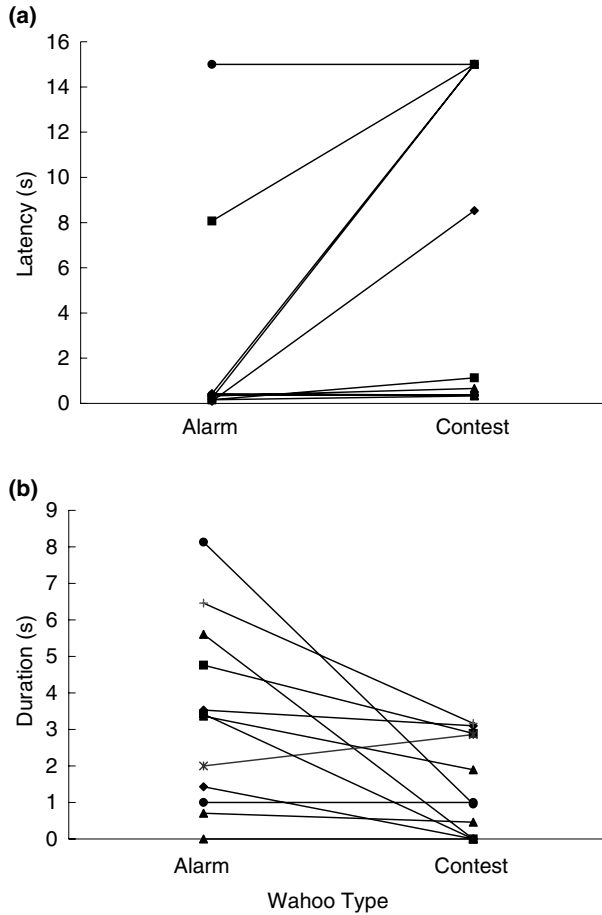


Fig. 1: Latency to orient towards concealed speaker (a) and duration of orientation towards speaker (b) by focal female baboons (n = 12) following playbacks of *alarm* and *contest* wahoos. Subjects who failed to respond at all were scored as having a latency of 15 s

Wilcoxon signed ranks test: n = 8, 4 ties, T = 1, p < 0.02). Subjects' latency to scan the area in any direction was also shorter following playback of *alarm* wahoos than *contest* wahoos, although not significantly so (Fig. 2; two-tailed Wilcoxon signed ranks test: n = 11, 1 tie, T = 15, p > 0.10). Subjects looked directly toward the speaker for a significantly longer period on average following *alarm* trials than following *contest* trials (Fig. 1; Wilcoxon signed ranks test: n = 10, 2 ties, T = 3, p < 0.01). Additionally, subjects scanned the area around them for a significantly longer period on average following *alarm* trials than following *contest* trials (Fig. 2; Wilcoxon signed ranks test: n = 12, T = 10, p < 0.05).

Only *alarm* wahoos caused females to flee; females ran or walked rapidly away from the speaker in four of the 12 *alarm* trials (mean ± SE latency:

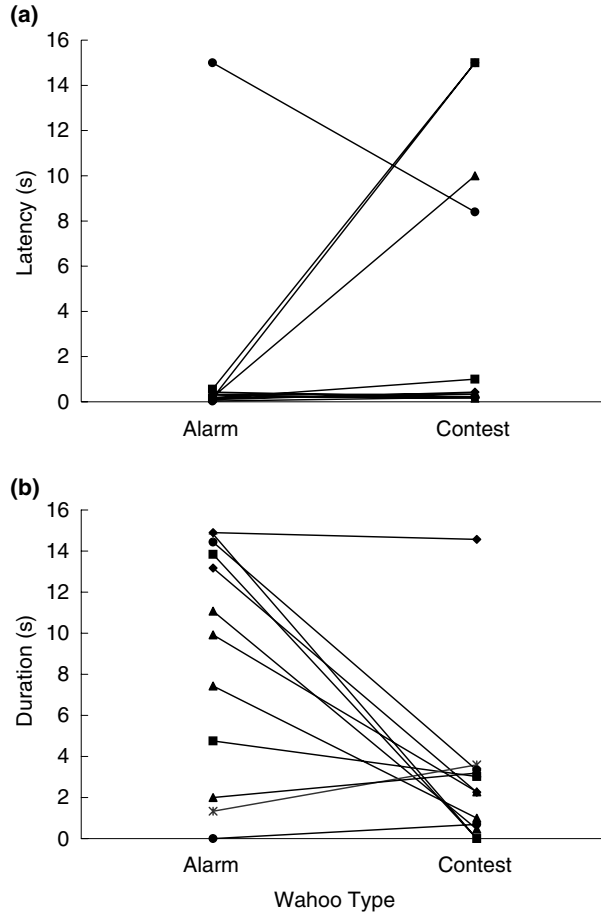


Fig. 2. Latency to onset of scanning (a) and duration of scanning (b) by focal female baboons ( $n = 12$ ) following playbacks of *alarm* and *contest* wahoos. Subjects who failed to respond at all were scored as having a latency of 15 s

$3.18 \pm 1.25$  s; mean  $\pm$  SE duration:  $10.35 \pm 2.72$  s), but in none of the 12 *contest* trials ( $X_1^2 = 4.80$ ,  $p < 0.05$ ).

Dependent offspring were not on their mother's back or stomach at playback onset in 14 paired trials on seven females. These infants were either actively retrieved or jumped onto their mother during five of the seven *alarm* trials but during none of the seven *contest* trials ( $X_1^2 = 7.97$ ,  $p = 0.005$ ). In two of the cases when the subject fled, the subject's infant was within 3 m of her at the time of playback, and the infant ran to the subject and jumped onto her before she moved away. In the other two cases when the subject fled, the infant was more than 3 m away from the subject. After recording onset, these subjects ran towards their infants and retrieved them before fleeing.



### Vocal Responses

Neither the female subject nor her dependent offspring produced any alarm calls during the trials, nor did they produce any alarm calls within the hour following the trials. Other group members, however, did vocalise during or following three *alarm* and three *contest* trials. In all cases, the types of vocalizations produced matched the category of calls broadcast during the playback trial.

Specifically, several individuals produced alarm calls during two of the *alarm* wahoo trials (in both cases, after the first call and before the second). Similarly, following one *contest* trial, three males produced *contest* wahoos (after the third call in the playback sequence and after the subject had finished responding, but within the 15-s post-playback period). Additionally, within the 1-h post-playback period, alarm calls were heard within 10 min following one *alarm* trial and a *contest* wahoo was heard within 1 min following one *contest* trial. Finally, a male produced *contest* wahoos and also chased the male heard signalling on the playback recording and several females within 2 min following another *contest* trial.

We should note that in the three trials in which playbacks elicited vocal responses within the 15-s post-playback period, the vocal response of other group members occurred after subjects had begun their own response. Moreover, removing these three trials on two females from the analysis (thus removing two sets of paired trials) did not affect the results (two-tailed Wilcoxon signed ranks test: duration of orientation towards speaker:  $n = 8$ , 2 ties,  $T = 2$ ,  $p < 0.05$ ; duration of scanning:  $n = 10$ ,  $T = 10$ ,  $p = 0.08$ ).

### Discussion

Female baboons responded significantly more strongly to playbacks of male *alarm* wahoos than to *contest* wahoos. Their latency to orient toward *alarm* wahoos was shorter than their latency to orient toward *contest* wahoos, and they oriented toward *alarm* wahoos for a significantly longer duration. Similarly, only *alarm* wahoos caused subjects to flee. *Alarm* wahoos and *contest* wahoos, therefore, appear to be functionally referential. Regardless of the mechanisms underlying call production, listeners apparently used subtle variations in acoustic cues to acquire information about different events in the environment (Cheney & Seyfarth 1996; Seyfarth & Cheney 2003).

These results add to a growing body of evidence suggesting that baboon listeners discriminate among subtypes of acoustically graded calls, although discrimination may be less clear in the overlap areas where call types intergrade. In addition to distinguishing *alarm* from *contest* wahoos, female baboons discriminate among typical, non-intermediate subtypes of barks (Fischer et al. 2001b) and grunts (Rendall et al. 1999).

Under natural conditions, females often flee and attempt to hide when males become involved in aggressive contests. Their relatively weak responses to

playbacks of *contest* wahoos in this study may have been due to several factors. First, signallers in our experiments were long-term resident males who were unlikely to be infanticidal. Secondly, under natural conditions females do not respond strongly to *contest* wahoos unless they occur in the context of highly conspicuous chases or escalated fights. In such circumstances, males produce wahoos at high rates and in long bouts (Kitchen et al. 2003). In contrast, our playback sequences consisted of only three calls, each separated by several seconds. Finally, playbacks were conducted in the absence of prior aggressive interactions or any visual cues of male aggression. As a result, while females oriented toward most *contest* wahoos, they did not respond strongly to them.

It might be argued that subjects responded more strongly to *alarm* than to *contest* wahoos not because *alarm* wahoos alert females to the proximity of a predator but because they occur less often and are therefore more novel. Although we cannot refute this argument entirely, it should be emphasized that *alarm* wahoos are not rare, particularly when nocturnal calls are considered. Moreover, because predation rates in this population are high (Cheney & Seyfarth unpubl. data), there is a certainly strong selective pressure to discriminate and attend to alarm calls. However, because both the functional reference argument and the novelty argument predict that females will respond more strongly to *alarm* than to *contest* wahoos, it is difficult to test precisely between the two hypotheses.

The experiments presented here do not reveal the exact mechanism used by subjects when responding to vocalizations. They do not indicate which acoustic features are most salient to subjects nor do they reveal whether *alarm* and *contest* wahoos elicit different responses because they prompt different emotional reactions, trigger different memories of past events, provide individuals with different sorts of information, or all of these (e.g. Premack 1972; Marler et al. 1992; Owren & Rendall 2001; Seyfarth & Cheney 2003). Previous research has indicated that infant baboons require experience before they can discriminate between females' *contact* and *alarm* barks (Fischer et al. 2000). Similarly, through processes of association and perhaps also by observing the responses of others, listeners attending to wahoos may learn when to escape into trees to avoid predators, when to adopt cryptic positions to avoid male aggression, and when it is safe to respond more weakly.

Because vocal production in non-human primates appears to be heavily constrained by the control subjects have over the structure of their calls (Jürgens 1995), listeners are under strong selective pressure to learn to differentiate among calls that are very similar acoustically but associated with markedly different events. Call rate clearly provides one means for listeners to distinguish *alarm* from *contest* wahoos, as do contextual and visual cues. Although the experiments presented here do not tell us exactly what information individuals acquire when they hear an *alarm* or *contest* wahoo, they do suggest that subjects discriminate between wahoo subtypes even when call rate, amplitude, bout length, and contextual and visual cues are controlled. It remains for future studies to determine whether females are equally skilled

at distinguishing intermediate forms of wahoos, and whether they can recognize the identities of individual signallers.

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