DYNAMIC CHANGES IN ALARM CALL STRUCTURE: A STRATEGY FOR REDUCING CONSPICUOUSNESS TO AVIAN PREDATORS?

by

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Summary

The design of many animal signals reflects the need to maximize signal efficacy while minimizing conspicuousness to eavesdroppers. The aerial alarm calls of birds have been a useful model system for exploring such evolutionary tradeoffs at the level of general call structure, but much less is known about changes in fine-scale signal characteristics over the course of an encounter with a potential predator. We analyzed variation in the alarm calls that male fowl, *Gallus gallus*, produced in response to raptor silhouettes moving overhead. Spectrogram cross-correlation was used to test for changes in structure over the course of a call bout. This analysis revealed that aerial alarm calls are individually distinctive and that they vary significantly from the first call to the second. We then measured single acoustic parameters, including the duration, dominant frequency and frequency bandwidth of each component in successive calls. Males almost invariably began the first call in a bout with a high amplitude broad-band pulse, which was followed by a much longer and highly variable sustained element. They then selectively reduced or eliminated the introductory pulse, while leaving other aspects of alarm structure unchanged. Recent work has shown that the introductory pulse is potentially costly because it has attributes that are readily localized by raptors. We suggest that male fowl have adaptive plasticity in alarm call structure, allowing them to manage short-term predation risk while continuing to signal to companions.

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Introduction

The structure of animal signals reflects a history of selection from both environmental characteristics (Morton, 1975; Wiley & Richards, 1978; Endler, 1993) and the sensory properties of potential receivers (Guilford & Dawkins, 1993; Bradbury & Vehrencamp, 1998; Endler & Basolo, 1998). Signal design is the product of tradeoffs between the need to influence intended receivers, such as mates and kin, and the cost of attracting unwelcome eavesdroppers, such as predators and parasites. For example, the sexual advertisement call of the male Tungara frog, *Physalaemus pustulosus*, consists of a tonal whine, followed sometimes by one or more broad-band elements (chucks) that increase attractiveness to conspecific females, but also make the caller more vulnerable to predatory bats. Males increase the number of chucks produced when they have adjacent competitors, and reduce or abolish these components when there is perceived predation risk. Signal complexity thus changes dynamically in response to variation in the costs and benefits of calling (Ryan *et al.*, 1982).

Alarm calls provide a model system for exploring such tradeoffs. The sender must evoke adaptive antipredator responses in companions, while minimizing any consequent increase in personal predation risk (Endler, 1993). Alarm call design should hence be strongly influenced by the perceptual abilities of both conspecifics and predators (Marler, 1955, 1957; Klump & Shalter, 1984; Klump *et al.*, 1986).

One way to control cost is by evolving signals that exploit sensory differences between intended and unintended receivers. For example, the ‘seeet’ aerial alarm call of the great tit, *Parus major*, has a dominant frequency of 6-8 kHz (Marler, 1955, 1957). Great tits are at least 15 dB more sensitive in this range than their principal avian predator, the sparrowhawk, *Accipiter nisus*, so ‘seeet’ calls that are clearly audible to nearby companions are much less likely to be detected by the raptor (Klump *et al.*, 1986). Aerial alarm calls have also been selected to reduce the conspicuousness of callers by decreasing localizability (Marler, 1955, 1957; Jones & Hill, 2001). Recent playback experiments have demonstrated that the aerial alarms of Australian honeyeaters and golden Sebright chickens are reliably detected by brown falcons, *Falco berigora*, but the probability of this predator successfully locating the source is much lower than for ground alarm calls of the same amplitude (Wood *et al.*, 2000). Taken together, these findings suggest that several distinct aspects of signal structure reflect an evolutionary tradeoff between the costs of calling (increased probability of attack) and the benefits (reduced predation risk for related companions).

Short-term changes in signalling behaviour can also be used to manage cost. Male fowl produce alarm calls selectively in the presence of companions and withhold them when alone (Gyger *et al.*, 1986). Experimental studies have explored the mechanisms underpinning this audience effect in some detail (Karakashian *et al.*, 1988; Evans & Marler, 1991, 1992, 1995), and similar sensitivity to social context has been described in other species (*e.g.* Cheney & Seyfarth, 1985; Sullivan, 1985). Calling that is costly for individuals but beneficial for other members of a group has also been important for exploring ultimate questions, such as the evolution of 'altruistic' behaviour (Maynard Smith, 1965).

Costs might also be controlled through moment-to-moment changes in alarm call structure. Previous analyses have concentrated principally upon variation in call usage according to eliciting conditions, exploring the relationship between alarm calls and factors such as predator type (*e.g.* birds: Walters, 1990; Evans *et al.*, 1993a; Jurisevic & Sanderson, 1994; sciurid rodents: Owings & Leger, 1980; Davis, 1984; primates: Seyfarth *et al.*, 1980; Macedonia, 1990; Pereira & Macedonia, 1991), or predation risk (*e.g.* birds: Maier, 1982; sciurid rodents: Leger *et al.*, 1980; Robinson, 1980; Owings & Hennessy, 1984; Blumstein & Armitage, 1997; primates: Macedonia & Evans, 1993). Considerable progress has been made in defining the type of information encoded in alarm calls (reviewed by Macedonia & Evans, 1993; Evans & Marler, 1995; Hauser, 1997), but less is known about signal design in these systems (Evans, 1997). In addition, there have been very few studies focusing on fine-scale structural variation within call class, as distinct from differences between call types. Nevertheless, there is some evidence from work on sciurid rodents that signallers might make short-term structural changes to reduce the cost of alarm calling. Bobac marmots, *Marmota bobac*, reduce call duration over the course of a bout, as risk of predation increases (Nikol'skii *et al.*, 1994). Similarly, golden marmots, *M. caudata aurea*, and alpine marmots, *M. marmota*, both give fewer whistles in each repetitive call as a predator approaches, which is likely to make them less conspicuous (Blumstein & Armitage, 1997). We are not aware of any analogous demonstration in birds of systematic variation in the fine structure of alarm calls that might function to reduce predation risk.

In the present study, we tested for changes in the structure of chicken aerial alarms over the course of responses to stimuli that simulated a predator flying overhead. These calls consist of an introductory pulse, which is characteristically short, broad-band, and relatively high amplitude, followed by a lower amplitude sustained element that can contain both narrow-band and broad-band components (Gyger *et al.*, 1987; Evans *et al.*, 1993a). Aerial alarm calls are testosterone-dependent (Gyger *et al.*, 1988) and are produced almost exclusively by males when conspecific receivers are present (Gyger *et al.*, 1986; Karakashian *et al.*, 1988; Evans & Marler, 1991). Playback of aerial alarm calls is sufficient to evoke appropriate antipredator responses; hens move into cover, crouch down with the feathers sleeked and scan upward as though to detect an approaching raptor (Evans *et al.*, 1993a).

Short broad-band calls are particularly easy to locate (Marler, 1955, 1957; Klump & Shalter, 1984) and hence likely to be costly. Consistent with this general pattern, falcons localize chicken ground alarm call bouts, which are composed of repeated broad-band pulses, much more successfully than aerial alarm calls (Wood *et al.*, 2000). We therefore predicted that the pulses at the beginning of aerial alarms would be selectively reduced after the initial response to an avian predator.

Methods

Subjects

We used archival recordings from experiments conducted over the last 12 years in which golden Sebright roosters have been shown computer-generated animations of raptor silhouettes moving across the screen of a large video monitor overhead (Fig. 1 in Evans & Marler, 1992). These experiments were designed to explore audience effects (Evans & Marler, 1992), referential signalling (Evans *et al.*, 1993a), predator recognition (Evans *et al.*, 1993b; Evans & Marler, 1995), and the influence of contextual cues on antipredator responses (Evans, unpublished data). Like the simple models used in classic ethological studies (*e.g.* Schleidt, 1961), hawk animations reliably evoke the full gamut of responses observed in interactions with real predators, including crouching, ‘freezing’ and aerial alarm calls (Fig. 1 in Evans *et al.*, 1993a). Variation in stimulus characteristics reliably affects the probability of calling, but there is no evidence for correlated changes in call structure (Evans *et al.*, 1993b).

Housing and experimental procedure have been described previously (Evans & Marler, 1992; Evans *et al.*, 1993a, b). Domesticated chicken strains have been derived from a subspecies of red junglefowl, *G. gallus gallus* (Fumihito *et al.*, 1994, 1996), and comparisons of call structure suggest that there are no differences between golden Sebrights and their wild progenitors.

Sound analysis

We digitized sound from the original analogue recordings (Nagra IV reel-to-reel, Marantz AMD420 cassette or Panasonic AG-7750 hi-fi video soundtrack) at 44.1 kHz, 16 bits, using a Digidesign AudioMedia III board and ProTools software (Digidesign, Avid Technology, Inc., Palo Alto, CA, USA). Digital spectrograms (FFT 1024 points, Hamming window; frequency resolution 174 Hz; 128 point steps with 87.5% overlap) were then generated with Canary 1.2.4 (Cornell Bioacoustics Laboratory) for 139 bouts of aerial alarm calling from 34 individual roosters.

Our hypothesis concerned whether males changed the spectral or temporal characteristics of their alarm calls over the course of a bout, so we eliminated sound files that only contained a single call and also those in which the quality of the original recording was poor. These two steps excluded 4 out of 34 males. Thirteen of the remaining males had produced only one bout of two calls, while 17 males contributed multiple call bouts, each consisting of either two or three calls. This latter group presented an opportunity for exploring the structure of longer alarm call sequences, so we selected three-call bouts from 11 individual males on the basis of signal-to-noise ratio. To choose recordings from the remaining six males, we first sorted sound files on the basis of recording quality and then classified the corresponding spectrograms according to spectral characteristics, scoring each call as primarily broad-band or narrow-band. When possible, we simply used the best recording. If two calls of the same bandwidth type were matched for quality, we picked one at random, while if two equivalent recordings were of different bandwidth types, we chose the one that was predominant in that male's set of recordings and hence better represented his typical aerial alarm.

The final set of digitized sounds selected for analysis contained bouts of calling from each of 30 individual roosters. All bouts contained at least two calls, and 11 contained three. We used a digital filter (high pass 250 Hz, low pass 12 kHz, inverse DFT) to improve the signal-to-noise ratio in each sound file and then examined call characteristics.

We tested for systematic structural changes over the course of alarm call bouts by using spectrogram cross-correlation, followed by measurement of selected frequency and temporal features. These two approaches are complementary. The first considers all aspects of signal structure and is sensitive to complex derived features (*e.g.* Guyomarc'h *et al.*, 1998), while the second facilitates identification of the subset of parameters that differ reliably from one call to the next.

Since digital spectrograms are visual representations of underlying numerical matrices, it is possible to use this information to measure acoustic similarity between whole sounds. Spectrogram cross-correlation involves calculating the normalized covariance between two frequency-time-amplitude matrices at successive time offsets (Clark *et al.*, 1987; Beeman, 1998). Cortopassi & Bradbury (2000) conclude that this technique performs well when analysis parameters (*e.g.* FFT length) are first optimized by inspection of spectrograms to verify that important time-frequency features are properly resolved, which is the strategy we have adopted here. Canary 1.2.4 was used to cross-correlate the spectrogram from each male's first and second call (1024 point FFT, Hamming window) with those from all other first and second calls, producing an array of 3600 peak correlation coefficients.

Our measurement procedure for single individual acoustic features is summarized in Fig. 1. We wished to identify *dominant frequency* (the spectral region containing the most signal energy), as this has been shown to predict audibility (*i.e.* probability of detection by conspecifics and predators; Klump *et al.*, 1986). Similarly, *frequency bandwidth* (the spectral range over which energy is distributed) influences signal localizability (*i.e.* probability

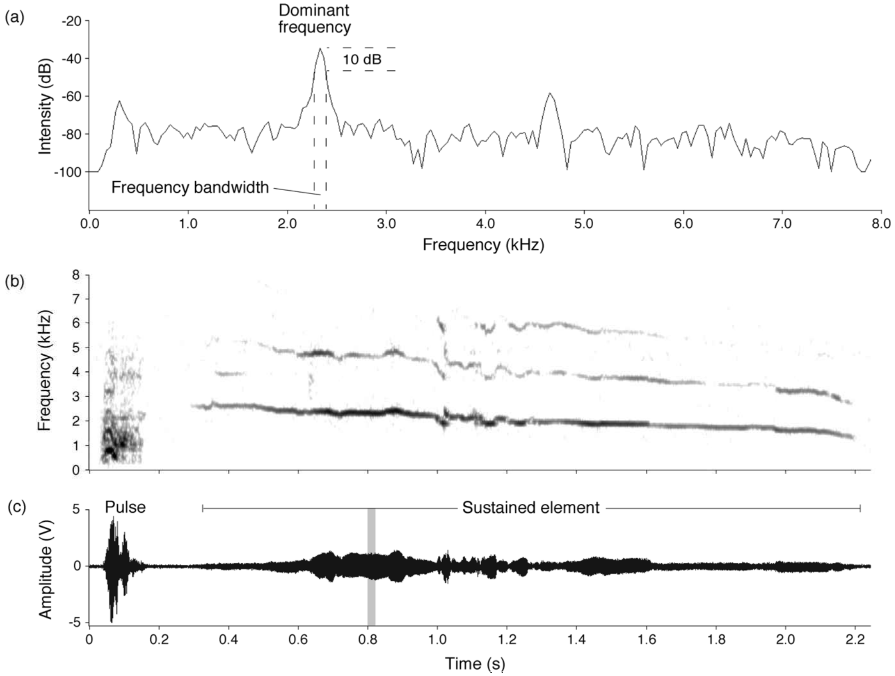

Fig. 1. Aerial alarm call structure. (a) Spectrum (1024 point FFT; frequency resolution 174 Hz) illustrating measurement of dominant frequency (most powerful component) and frequency bandwidth (−10 dB). (b) Spectrogram of an alarm call (512 point FFTs, 99.8% overlap; frequency resolution 349.7 Hz). Gray scale represents an amplitude range of 40 dB. (c) Oscillogram showing duration measurements. The introductory pulse and sustained element are clearly distinct. Vertical gray band indicates the waveform region from which the spectrum (a) was calculated.

of receivers determining the spatial location of the caller; Marler, 1955, 1957; Wood *et al.*, 2000). We used Canary 1.2.4 to measure pulse dominant frequency and frequency bandwidth (−10 dB) by calculating a 1024 point FFT (Hamming window) at the approximate temporal midpoint of each alarm call component (Fig. 1). Sustained elements did not always have a uniform structure, but could be made up of a series of distinct units, delineated by abrupt changes in frequency bandwidth. To ensure that estimates of spectral characteristics would not largely reflect the temporal location sampled, we did FFTs at the temporal midpoint of each component separately, and then calculated a weighted mean frequency bandwidth and a weighted mean dominant frequency for the whole sustained element. As changes need not be (and were not predicted to be) exclusively spectral, we also measured the total duration of each alarm call, and those of the introductory pulse and of the sustained element separately.

Data analysis

We analyzed the array of spectrogram correlation coefficients using the multi-dimensional scaling (MDS) procedure in SPSS 10.0.7a (SPSS Inc.). MDS is a set of mathematical techniques which reduce large data arrays to a spatial model of x dimensions, thereby facilitating detection of similarity between objects (Kruskal & Wish, 1978). In our application, MDS was used to obtain an economical summary of variation among spectrogram matrices. Calls with similar overall structure will receive similar scores on each of the dimensions produced and hence will be located close together in the spatial model. The success of an MDS solution can be ascertained from the stress and r^2 values produced. The lower the stress value for a given number of dimensions, the better the model; we used the conventional value of 0.15 as a cut-off. Likewise, the higher the r^2 value, the better the relationship between variation in the original data and distances in the spatial model. A multivariate analysis of variance (MANOVA), with the dimension scores as the dependent variables and call order as the grouping variable, was used to test for possible differences in the structure of first and second calls.

We anticipated that males would reduce or eliminate the introductory pulse after the initial alarm call, as this element should contribute disproportionally to caller conspicuousness (see Introduction). Pairwise comparisons based on this *a priori* prediction were one-tailed; all other comparisons were two-tailed. We first assessed whether males were less likely to produce a pulse after their first call using a test for significance of difference between two proportions (Bruning & Kintz, 1977). Comparisons of single acoustic characteristics were conducted with non-parametric tests using Statview 5.0 (SAS Institute, 1998), as the data were not normally distributed and did not meet the assumption of equal variance. Changes in structure across the whole aerial alarm call bout were assessed with a Kruskal-Wallis H-test. Wilcoxon signed-rank tests were then used for subsequent planned pairwise comparisons between first, second and third calls. The alpha level was set at 0.05 throughout.

Results

Spectrogram cross-correlation

Analysis of the 60×60 frequency-time-amplitude matrix produced by cross-correlation using MDS showed that the data were best represented by a four-dimensional solution (stress $= 0.129$, $r^2 = 0.895$). The initial MANOVA analysis performed on these data was non-significant (Wilks' Lambda $p = 0.97$) suggesting that there were no consistent changes in overall structure between first and second alarm calls.

Further investigation, however, revealed that there was substantial individual variation in the MDS scores, particularly on the first dimension. The intra-class correlation for this dimension of 0.85 (95% confidence interval 0.76-0.95) indicated that approximately 85% of the variation in the score was due to between-bird differences (the corresponding intra-class correlations for dimensions 2-4 were 0.25 [0-0.59], 0.55 [0.30-0.80] and 0.72

[0.55-0.90]). This result suggested that aerial alarm calls are individually distinctive and that an effect of call position might be obscured by consistent differences between males. To remove the effects of individual variation, we carried out a multivariate test using differences in MDS dimension scores between first and second calls. This was significant (Wilks' Lambda $p = 0.027$). The univariate result for the first MDS dimension was also significant ($F_{1,29} = 13.8$, $p = 0.001$). It should be borne in mind, however, that these differences, though statistically significant, are small in comparison to overall differences between birds on the first MDS dimension.

In summary, spectrogram cross-correlation reveals that there is a reliable change in structure from the first alarm call in a bout to the second, although this is only significant once the individual variation between males is taken into account.

Variation in usage and structure of the introductory pulse

Pulses were reliably present at the beginning of the first aerial alarm call of a bout, but almost all of the males (27/30) reduced or eliminated this element in their second and subsequent alarms. Figure 2 presents representative spectrograms illustrating this change in signal structure. The remaining three males produced a double pulse in the second call. There is considerable individual acoustic variation in male *G. gallus* alarm calls (Fig. 2), but these were the only exemplars we had for these males, so we were unable to test whether double-pulses were a reliable individual characteristic. Nevertheless, since only 3/30 males produced double pulses they were clearly unusual at the population level. We analyzed the data set in two ways, first considering the 27 males with typical call structure and then including the three aberrant males. Results were similar in all but one parameter. We consider first data from the 90% of males who did not double pulse.

The proportion of second alarm calls containing a pulse was significantly less than that of first alarm calls (Fig. 3a; test for significance of difference between two proportions: $z = -3.5$, $p < 0.00005$). Mean pulse duration was also significantly reduced from the first to the second call in a bout (Wilcoxon signed-rank test, one-tailed: $z = -4.03$, $N = 27$, $p < 0.00005$). Given that 45% of males eliminated the pulse in the second call (and hence contributed a duration score of 0 ms), we next considered the subset of males whose second calls had pulses to determine whether the significant reduction

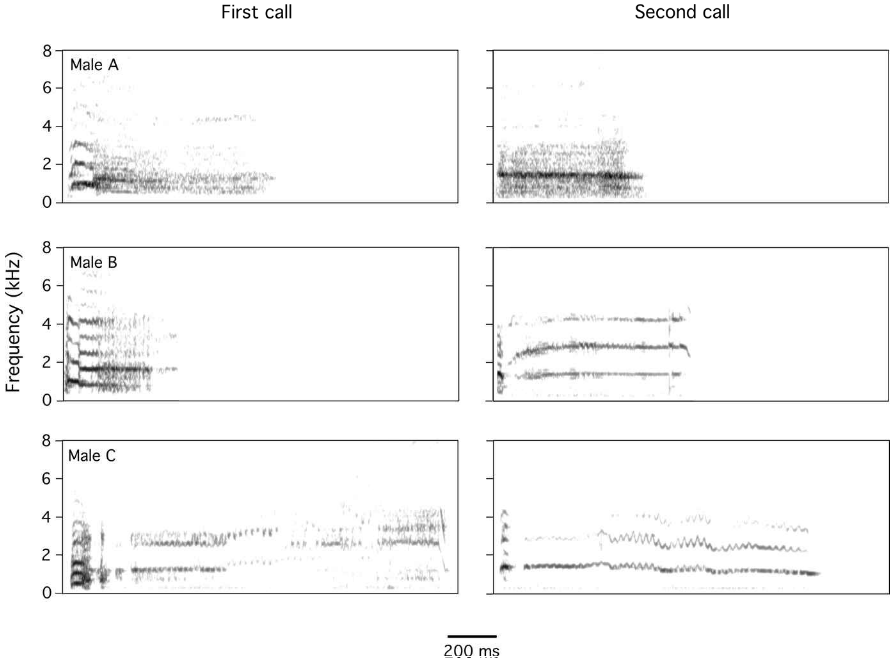

Fig. 2. Spectrograms of representative aerial alarm calls from three males. Note that the introductory pulse was either eliminated (Male A) or substantially reduced (Males B and C) after the first call in each bout.

in mean pulse duration apparent in the whole population was just a consequence of some individuals eliminating this element entirely. These comparisons revealed that, even when the pulse was retained, it was significantly briefer in the second call (Fig. 3b; $z = -2.44$, $N = 15$, $p = 0.007$).

Similar patterns were apparent in the structure of aerial alarms produced by the minority of males who called three times. While all 11 of these individuals produced a pulse in the first call, only seven pulsed in the second call, and three in the third call. The position of an alarm call in the bout (first, second or third) had a significant effect on pulse duration (Kruskal-Wallis H-test: $H = 11.4$, df $= 2$, $p = 0.033$). In this case, 36% of males dropped the pulse in the second call and 72% dropped it in the third call. Pairwise comparisons reveal that pulse duration was significantly reduced from the first call to the second (Wilcoxon signed-rank test, one-tailed: $z = -1.689$, $N = 11$, $p = 0.046$), and between the first call and the third ($z = -2.845$, $N = 11$, $p = 0.002$), but there was no significant difference in pulse duration between the second and the third calls ($z = -1.540$, $N = 11$, $p = 0.062$).

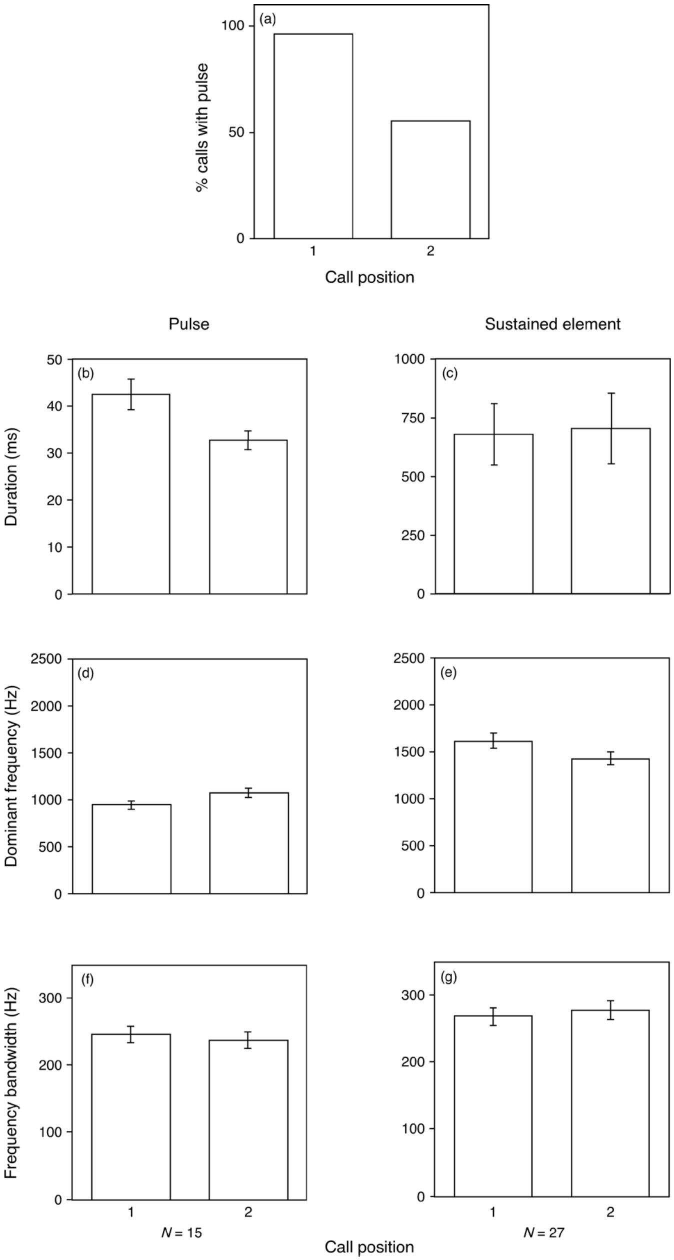

Fig. 3. (a) Probability of aerial alarm calls having an introductory pulse. Panels (b)-(g) depict results from measurements of single acoustic parameters (mean ± SE) as a function of element and call position. See text for details.

We also explored whether there were systematic changes in pulse spectral properties by examining the subset of bouts in which this element was retained in the second call. There was no significant difference in pulse dominant frequency between first and second alarm calls, (Fig. 3d; Wilcoxon signed-rank test, one-tailed: $z = -0.68$, $N = 15$, $p = 0.496$). Similarly, there was no significant variation in pulse frequency bandwidth (Fig. 3f; $z = -0.34$, $N = 15$, $p = 0.733$). Meaningful comparisons were not possible for three-call bouts, as only seven of these had pulses in the second call and just two had pulses in both second and third calls.

In summary, analyses of pulse characteristics suggest that males were significantly less likely to include this component after the initial aerial alarm and that, when they were retained, pulses were significantly briefer. Systematic changes were restricted to the temporal domain. We could find no evidence of variation in dominant frequency (which affects audibility in some systems) or in frequency bandwidth (which is a correlate of localizability).

Properties of the sustained element

To test whether the reduction in introductory pulse duration was selective, or whether it simply reflected an overall reduction in the duration of all alarm call components, we next conducted an analogous series of tests for the sustained element. There was no significant difference in duration of this component between the first call and the second (Fig. 3c; $z = -0.553$, $N = 27$, $p = 0.29$), or over the course of the whole bout for males that called three times (Kruskal-Wallis H-test: $H = 0.041$, df $= 2$, $p = 0.980$).

There was a small difference in sustained element dominant frequency between first and second calls (Fig. 3e; $z = -2.045$, $N = 27$, $p = 0.041$) when we considered the males who did not produce double pulses, but this effect was no longer significant when we tested the whole population ($z = -1.870$, $N = 30$, $p = 0.061$). This was the only variable in our analyses that differed in significance between the two data sets and the difference is clearly not robust, as it was abolished by the addition of only three males. We are consequently reluctant to interpret this suggestion of variation in dominant frequency. There were no significant differences between the first and second calls in mean frequency bandwidth (Fig. 3g; $z = -0.841$, $N = 27$, $p = 0.4$). There were also no significant differences in either mean dominant frequency (Kruskal-Wallis H-test: $H = 0.054$, df $= 2$, $p = 0.973$) or mean frequency bandwidth ($H = 2.201$, df $= 2$, $p = 0.333$) in the smaller set of three-call bouts.

Discussion

Our results suggest that there is adaptive plasticity in the structure of chicken aerial alarm calls. Spectrogram cross-correlation reveals that alarms are individually distinctive and shows that, once this obscuring factor is removed, there is a reliable change over the course of a call bout. Measurements of single acoustic parameters demonstrate that males reduced or eliminated the introductory pulse after the initial response to a simulated predator (Fig. 2, Fig. 3a, b). We could detect no comparable changes in the sustained element (Fig. 2, Fig. 3c, e, g), which allows us to reject the possibility that variation in pulse characteristics might simply reflect more global variation in call structure. We conclude that changes to the introductory pulse were highly selective. Perceptual testing of raptors has shown that calls with temporal and spectral characteristics like those of the pulse are readily localized and hence likely to be relatively costly (Wood *et al.*, 2000; Jones & Hill, 2001; see Introduction). Taken together, these findings are consistent with the idea that males may use dynamic changes in aerial alarm call structure to reduce their conspicuousness, while continuing to warn companions about a predation threat.

The structure of aerial alarm calls typically functions to minimize the cost associated with signalling, either by exploiting differences in acoustic spectral sensitivity between avian predators and conspecifics (Klump & Shalter, 1984; Klump *et al.*, 1986), or by minimizing localization cues (Marler, 1955, 1957; Wood *et al.*, 2000). These properties presumably reflect a long evolutionary history of selection from predators with good auditory acuity. It is also well established that costs can be controlled over the short-term by signalling only when appropriate receivers are present (Gyger *et al.*, 1986; Karakashian *et al.*, 1988; Evans & Marler, 1991, 1992), and by inhibiting calling when predation risk is high (Ryan *et al.*, 1982; Mougeot & Bretagnolle, 2000). Energetic costs are unlikely to be important in fowl — crowing, which is a loud and frequently repeated territorial signal, does not appreciably increase metabolic rate (Chappell *et al.*, 1995; Horn *et al.*, 1995).

It has been shown experimentally that production of male *Gallus gallus* aerial alarm calls is dependent upon simple stimulus parameters such as apparent size (angle subtended at the bird's eye) and speed (Evans *et al.*, 1993b). This perceptual strategy requires minimal processing and facilitates a fast response to a perceived predator, which is clearly adaptive when dealing with a rapidly approaching raptor. However, call specificity may be reduced as a consequence (Gyger *et al.*, 1987; Evans *et al.*, 1993b; Evans & Marler, 1995). Innocuous stimuli such as small, low-flying passerines can have properties similar to those of a large raptor flying at a higher altitude, and can thus elicit aerial alarm calls (Evans *et al.*, 1993b). Although there are systematic changes in non-vocal response (crouching, 'freezing') as the threat posed by a simulated aerial predator is increased (Evans *et al.*, 1993b), production of aerial alarm calls seems to be categorical in nature; there is no evidence for gradual changes in signal structure such as those that might encode response urgency (*e.g.* Owings & Hennessy, 1984; Roux *et al.*, 2001).

Dynamic variation in alarm call structure provides animals with an additional, and quite distinct, strategy for managing risk by decreasing conspicuousness. Marmots reduce call duration (Nikol'skii *et al.*, 1994) or the number of alarms given in response to increasing predation threat (Blumstein & Armitage, 1997). To our knowledge, the present study provides the first evidence for this type of signalling flexibility in birds. In *G. gallus*, plasticity in alarm call structure seems to be largely restricted to the temporal domain, which may reflect limitations inherent in syringeal structure or motor control (*e.g.* Gaunt & Nowicki, 1998), or the effects of non-vocal antipredator responses elicited by threat from an aerial predator (*i.e.* fixation, crouching and twisting the head to track the predator with one eye). Our results suggest that aerial alarm calling in this species may reveal multiple adaptations for minimizing cost in the face of environmental and physiological constraints, both at the level of overall signal design, and through more subtle short-term changes in structure within call bouts.

If the introductory pulse is attenuated to control cost when calls are repeated, how are we to explain its reliable presence in the first aerial alarm in a bout? It is likely that this element enhances signal efficacy (Guilford & Dawkins, 1993). The structure of the pulse is consistent with an alerting function; such components are characteristically simple, intense and brief (Endler, 1993). For example, the introductory notes of some oscine songs are designed to engage the attention of conspecifics, and these differ reliably in structure from those that follow (Becker, 1982; Soha & Marler, 2000). Playback experiments demonstrate that the initial reaction of hens to aerial alarm calls is to orient toward the loudspeaker (Evans *et al.*, 1993a) and the physical characteristics of the introductory pulse — in particular, rapid amplitude rise time — are those that have been shown most effectively to interrupt behaviour in experiments using simple acoustic stimuli (Fleshler, 1965;

Graham, 1979). Other studies have shown that the non-vocal antipredator responses of males also increase monotonically with the apparent size and speed of a hawk silhouette (Evans *et al.*, 1993b). It is likely that by locating the caller and observing such behaviour, companions can obtain contextual cues (Leger, 1993) that supplement the information provided by the call, and perhaps also enhance their ability to locate and respond appropriately to the predator (Evans, 1997).

It is also relevant to ask why almost half of the males produced no introductory pulse in the second call. It would be most adaptive to do this if the first pulse had already attracted the attention of the target audience. The experiments in which these calls were recorded focused on the response of males to raptor stimuli — audiences were provided primarily to ensure appropriate conditions for production of aerial alarms. It would be interesting to explore the possibility that males are more likely to include a pulse in the second call when the receiver is inattentive.

We suggest that dynamic changes in alarm call structure are best viewed as a tradeoff in which males attempt to further reduce predation risk for companions by continuing to call, perhaps as an example of tonic communication (Schleidt, 1973; Owings *et al.*, 1986), while at the same time managing their own predation risk.

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