



Universität
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Vocal Communication in the Banded Mongoose

Complexity of information coding

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- Introduction
- Study species/site
- Vocal repertoire
- Vocal cues
- Call sequences
- General discussion

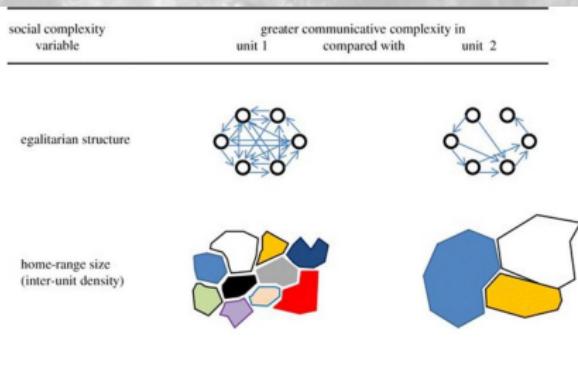
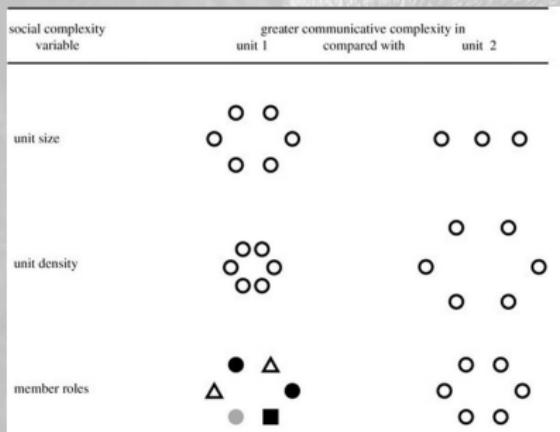
The Expression of the Emotions in Man and Animals.

'With social animals, the power of intercommunication between the members of the same community, and with other species, between the opposite sexes, as well as between the young and the old, is of the highest importance to them. This is generally affected by means of the voice, but it is certain that gestures and expressions are to a certain extent mutually intelligible.'

Darwin 1872, p. 60

Social complexity

- Social complexity hypothesis
 - Social groups
 - Cognitive skills



(Whitten and Byrne, 1988; McComb and Semple, 2005; Freeberg et al, 2012)

The evolution of communication.

'...the richest elaboration of systems of social communication should be expected in intra-specific relationships, especially where trends towards increasing inter-individual cooperation converge with the emergence of social groupings consisting of close kin.'

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Social complexity and vocal repertoire complexity

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The evolution of male loud calls among mangabeys and baboons.

'...the value to a signaler of broadcasting information to recipients, and thus the degree to which selection favors specialized 'information-transfer' abilities, depend[s] on the social system.'

Waser 1982, p. 118

Social complexity

- Social complexity drives the evolution of communicative complexity
- Likely in all 3 modalities
 - Vocal
 - Visual
 - Olfactory

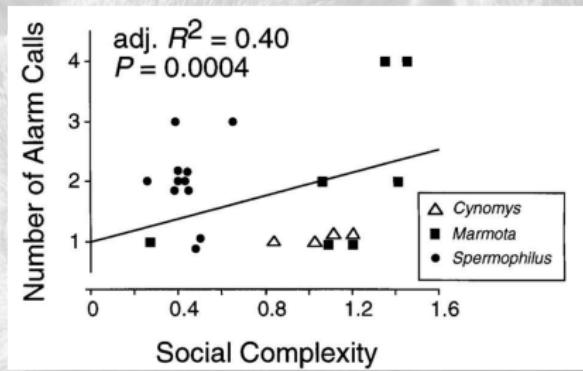
(Marler, 1977; Hauser, 1996; Freeberg et al, 2012)

Social complexity and communicative e complexity

- Focus of recent research



Social complexity and vocal complexity

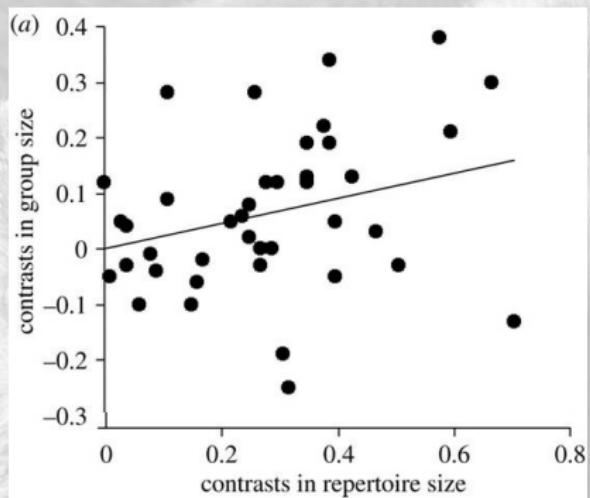


Blumstein and Armitage, 1997



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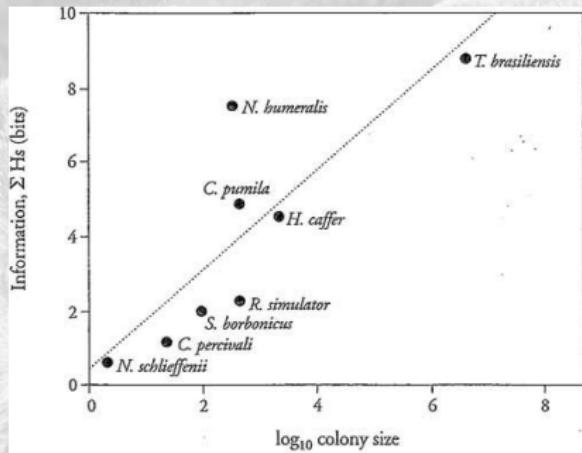
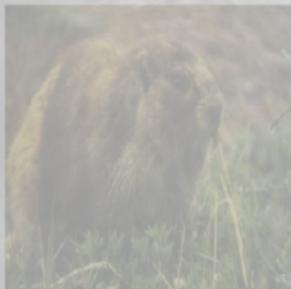


McComb and Semple, 2005



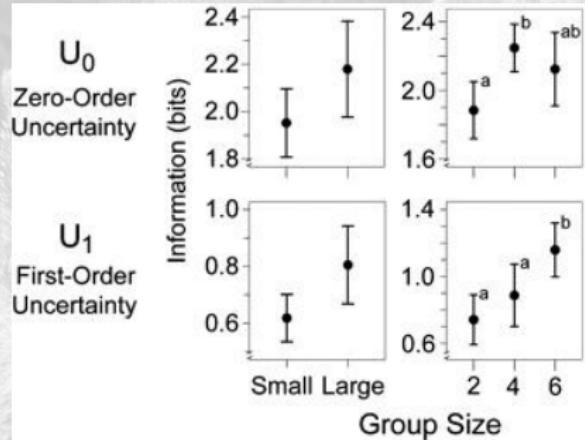
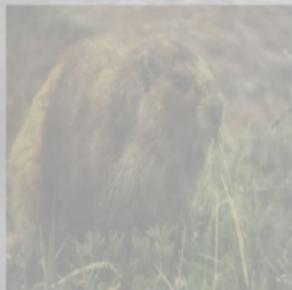
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Freeberg, 2006



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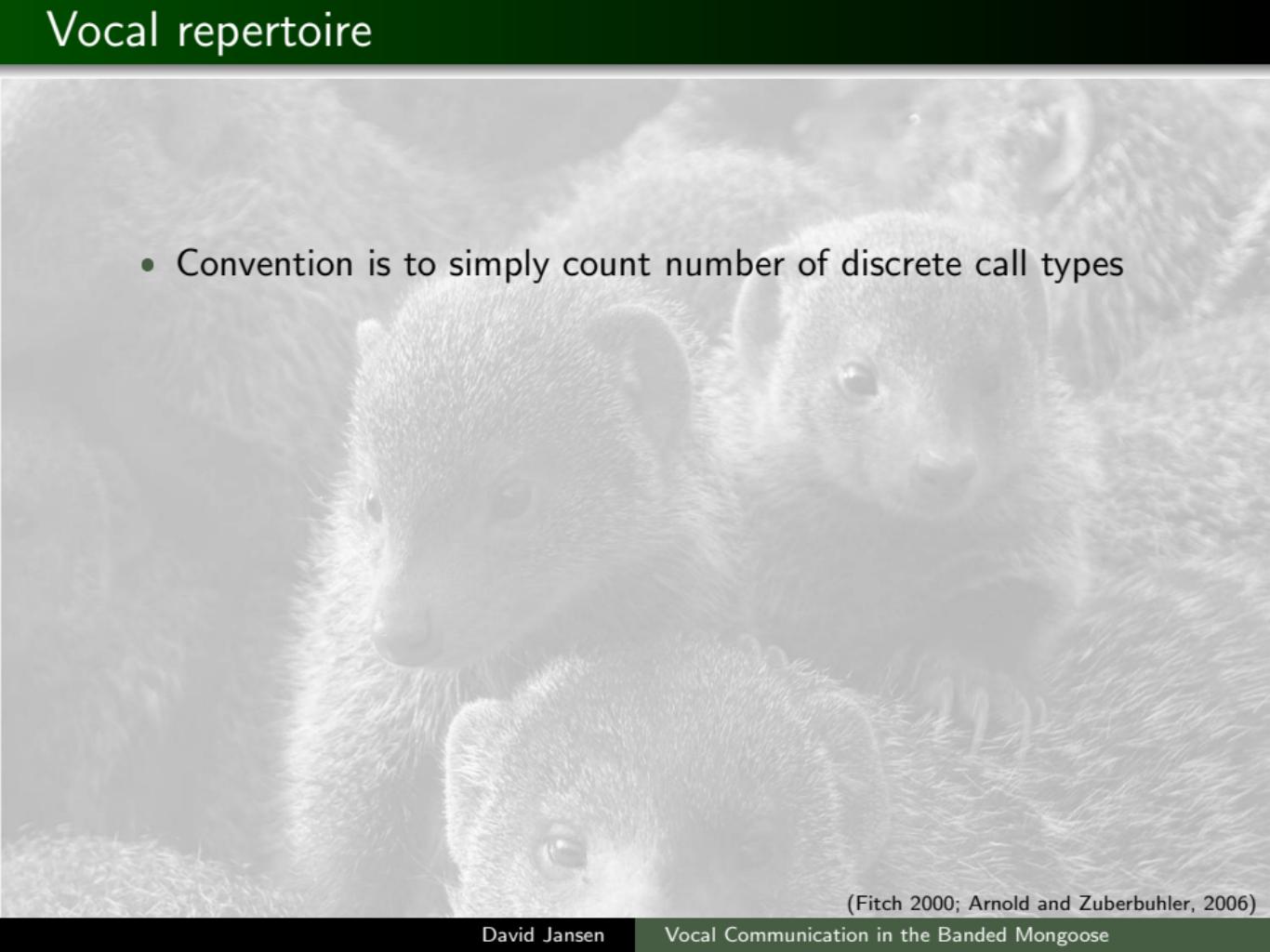
Social complexity and communicative e complexity

- Focus of recent research
- Limited or partial evidence



Vocal repertoire

- Convention is to simply count number of discrete call types



(Fitch 2000; Arnold and Zuberbuhler, 2006)

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 - Campbell's monkeys (*Cercopithecus campbelli campbelli*)
 - Putty-nosed monkeys (*Cercopithecus nictitans martini*)
- But what about vocal cues?

(Fitch 2000; Arnold and Zuberbuhler, 2006)

Vocal cues

- Individual identity most commonly shown vocal cue



Vocal cues

- Individual identity most commonly shown vocal cue, but also vocal cues for:
 - Parent-offspring recognition
 - Group
 - Sex
 - Male quality
 - Reproductive state



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⇒ These all provide potential additional information to receivers



Social complexity and vocal cues

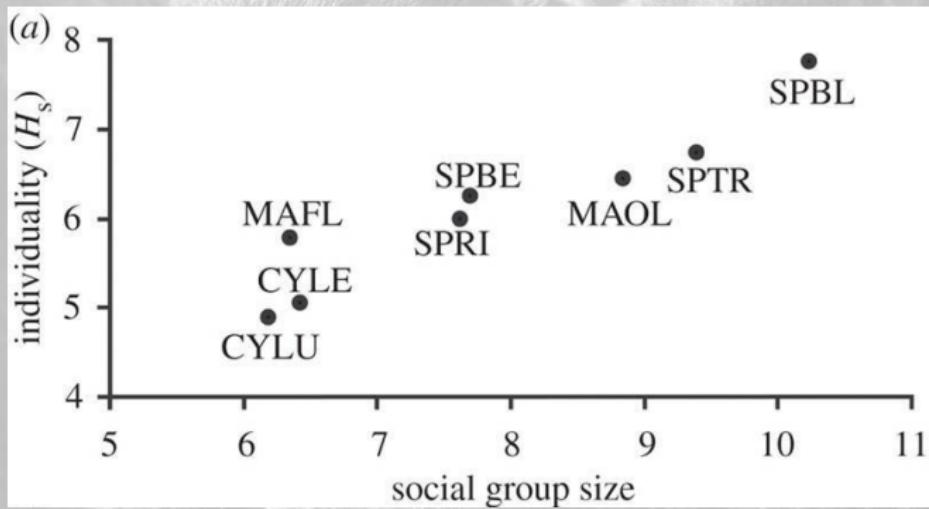
- Individuality is expected to evolve with group size
 - Social group size hypothesised to drive the evolution of individual signatures



(Beecher, 1989; Pollard & Blumstein, 2011/2012)

Social complexity and vocal cues

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Social complexity and vocal repertoire complexity

- Focus of recent research
- Limited or partial evidence
- Need for more comparisons



Social complexity and vocal repertoire complexity

- Focus of recent research
- Limited or partial evidence
- Need for more comparisons
 - Lemurs
 - Mongooses
 - Solitary
 - Family groups
 - Cooperative breeders



Study species and study site

- Banded mongoose *Mungos mungo*
- Approx. 2kg
- Communally breeding
- Groups of mixed sex with 7 to 45 individuals
- No clear dominance hierarchy



Banded mongoose - Vocalisations

- Vocal repertoire of captive study
 - High degree of variability and graded
 - 9 different vocalisations
 - Two close call types

(Messeri et al, 1987)

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 - Individual signature in close call

Banded mongoose - Vocalisations

- Vocal repertoire of captive study
 - High degree of variability and graded
 - 9 different vocalisations
 - Two close call types
- Previous observations in the field
 - Individual signature in close call
 - Graded recruitment calls

Study site

- Queen Elisabeth National Park, Uganda
- Banded Mongoose Research Station (since 1995)
- 4-6 habituated groups
- Approx. 200 individuals
- All individuals individually marked
- Approx. 30 - 50 habituated to recording microphone at $\leq 2\text{m}$



Methods - field work

- *Ad libitum*
- 5 minutes focal watches
- Record behaviour and associated calls
- Close call variations
- Call sequences

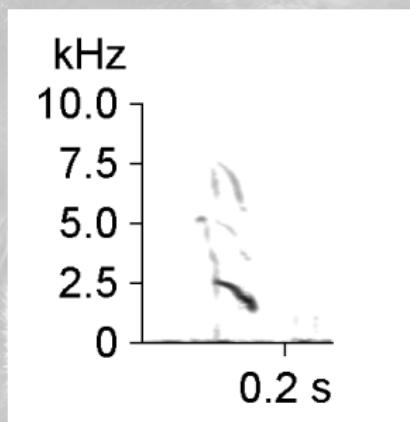
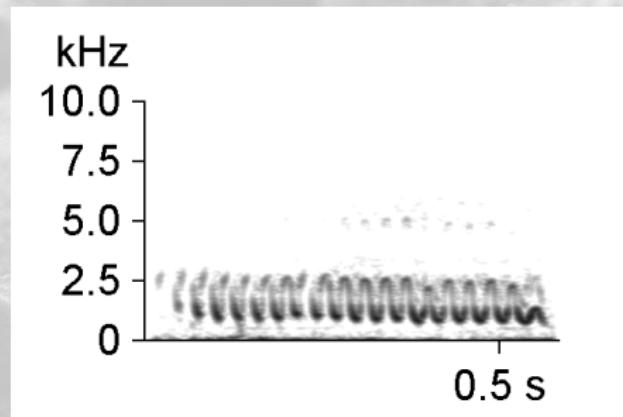
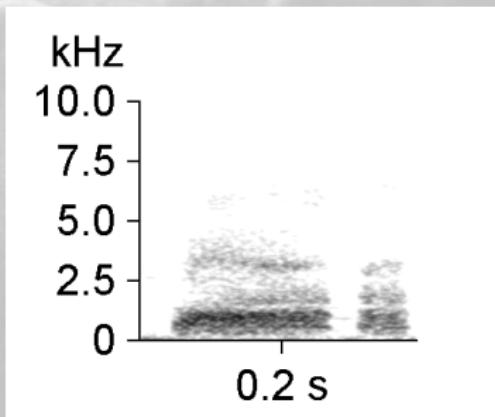


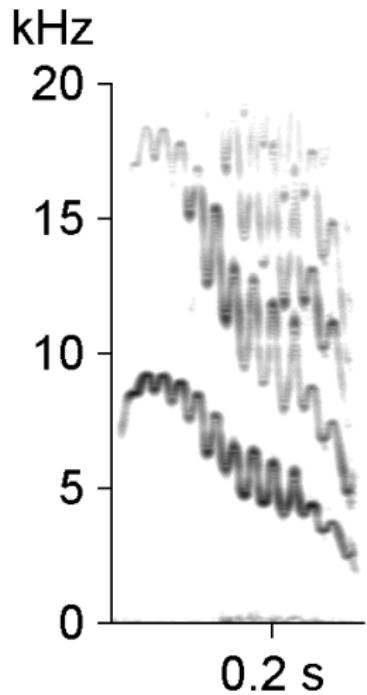
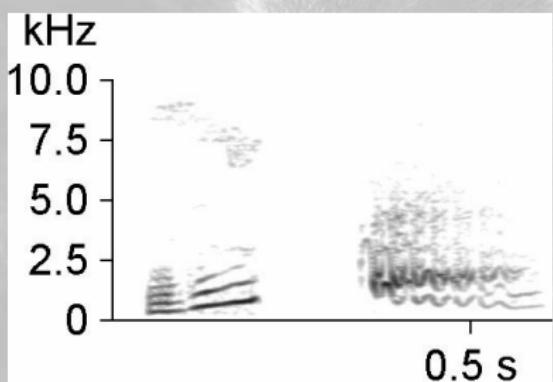
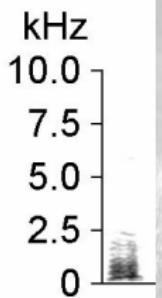
Methods - statistical analysis

- Mixed effect models
- Variance inflation factor
- DFA analyses with stepwise variable selection
- Permuted DFA for nonindependent data
- Bootstrapping analysis to test for significance

Result - Vocal repertoire

- 14 adult call types
- Calls show high degree of variability





Result - Vocal repertoire

- 14 adult call types
- Several new call types
- Calls show high degree of variability
- Calls in 4 different behavioural contexts

Behaviour contexts	Number of call types
Cohesion/movement	3
Resource calls	4
Social calls	4
Calls of context in danger	3

- Additionally 6 pup vocalisations

Discussion - vocal repertoire

- Graded vocal repertoire
- Complicated categorisation
- Morton motivational rules
- Differences with other social mongooses

Close calls

- Most commonly emitted call type
- Soft short distance vocalisation
- Likely related to maintaining group cohesion
- Individually distinct
- Additional variation

Research questions - Close calls

- What vocal cues are encoded in close calls?

Research questions - Close calls

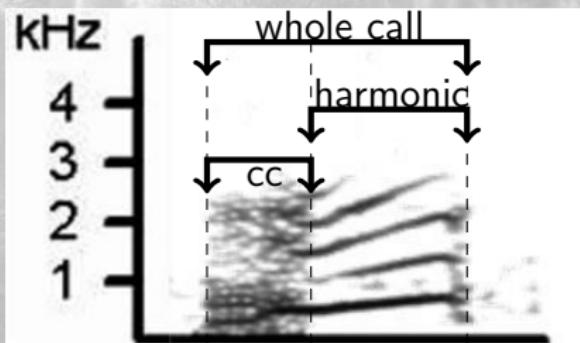
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Research questions - Close calls

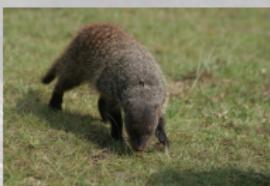
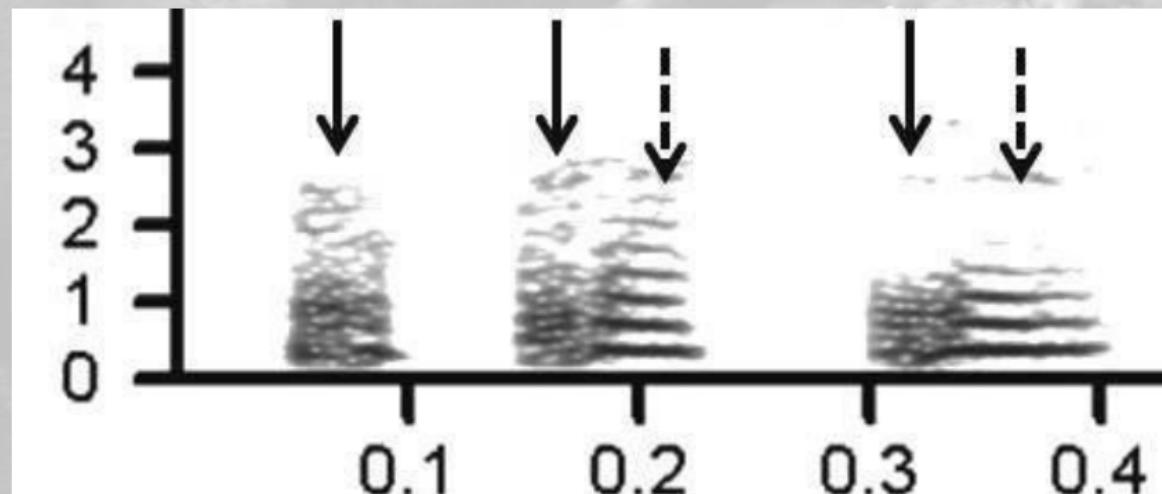
- What vocal cues are encoded in close calls?
- How is the individual signature encoded in a graded call?
- Is the additional variation correlated with behaviour?

Methods - Close calls

- Assigned labels to call parts
 - Whole call
 - Noisy part (cc)
 - Harmonic part (if present)
- 16 parameters
 - Spectral parameters
 - Temporal



Results - Spectrogram



(Jansen et al 2012)

Results - individual signature

Group	#*	Random (%)†	CV-values (%)		
			Whole call	Noisy part	Harmonic
1B	8	12.5	48.1***	45.0***	25.0
1H	14	7	26.1*	40.0***	11.4
11	7	14	42.0***	48.0***	22.0
15	7	14	61.5***	61.1***	22.5

* Number of individuals tested

† p -values are derived by bootstrapping (Müller and Manser, 2008); * $p \leq 0.05$, ** $p \leq 0.01$,

*** $p \leq 0.001$

(Jansen et al 2012)

Results - behavioural cue

Part analyzed	Behavior	Individuals	ncce [‡]
Whole call	digging–searching	30	3.340*
	digging–moving	25	40.640***
	searching–moving	20	30.610***
Noisy part	digging–searching	30	1.500
	digging–moving	25	34.850
	searching–moving	20	23.100
Harmonic part	digging–searching	18	78.040***
	digging–moving	30	77.440***
	searching–moving	30	67.600**

[‡] The results of the pDFA is the number of correctly cross-classified elements (ncce).

* $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Temporal segregation of vocal cues

- Banded mongoose close calls first quantification in an animal vocalisations for:

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 - An identity cue as discrete element within a single call

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Temporal segregation of vocal cues

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 - An identity cue as discrete element within a single call
 - 'Segregation of information' within a call type
 - Temporally separated behavioural cue
 - 'Vowel-like' segmentation with an animal vocalisation

Call sequences

- Predominately shown in predation contexts
- Hypothesised to be prevalent in affiliative and social contexts
- Mainly been shown in primates
- Predominately investigated for the possible link to evolution of language

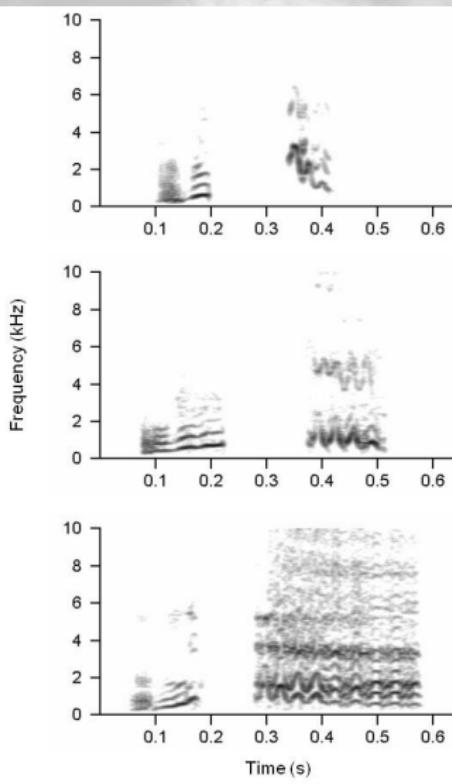
(Lemasson and Hausberger, 2011; Candiotti et al, 2012)

Research questions - Call sequences

- Are close calls used in call sequences?
- Is the individual cue in the close call maintained?
- In which behavioural contexts are the call sequences used?

Call sequences - Spectrogram

Excitement -



Lead -

Lost -



(Jansen et al to be submitted)

Results - Call sequences

Call type	Context
Excitement	Emitted when encountering wet ground/onset of rain
Lead	Initiation and coordination of group movement
Lost	Emitted when separated from their group

Results - DFA call sequences

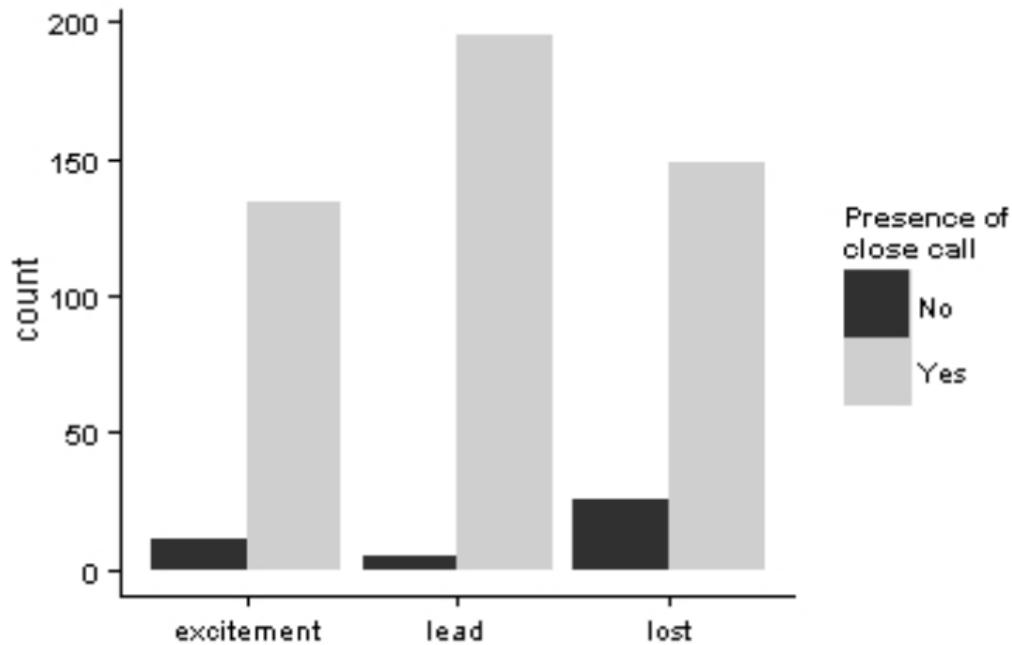
Call types	Predicted membership			Total
	Excitement	Lead	Lost	
Excitement	72.7	27.3	0	100
Lead	3.7	81.5	14.8	100
Lost	8.7	21.7	69.6	100

(Jansen et al to be submitted)

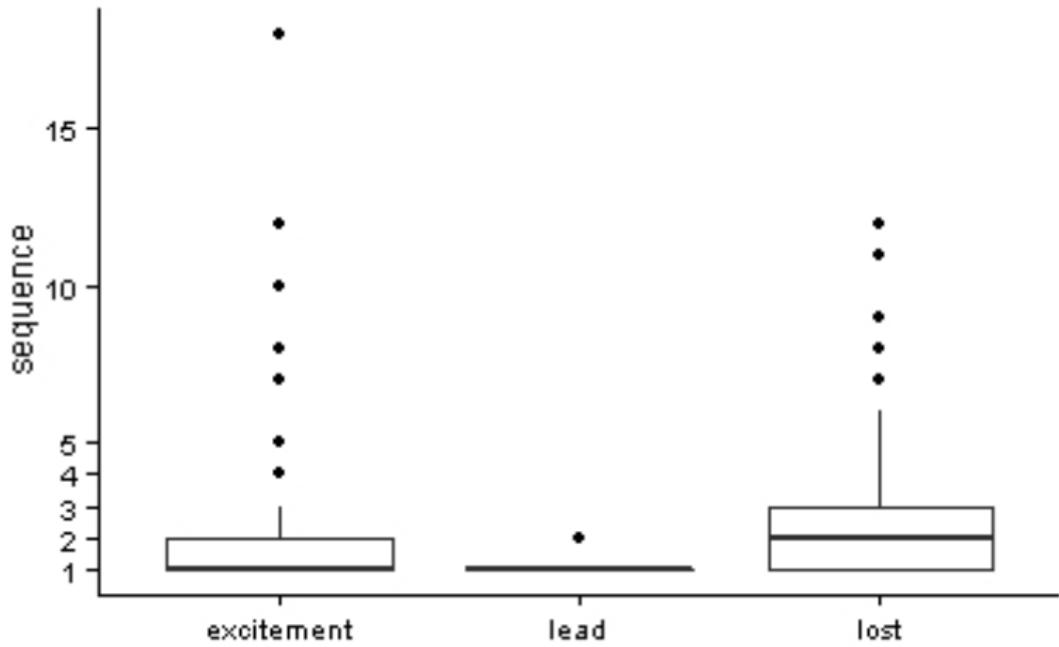
Call types	Observed behavioural context						Total
	Excitement	Leading	Lost	Foraging	Other		
Close call	-	-	-	21	-	-	21
Excitement	9	1	-	-	1	-	11
Lead	-	26	1	4	-	-	31
Lost	-	3	17	2	3	-	25

(Jansen et al to be submitted)

Results - call sequences



Results - call sequences



Discussion - Call sequences

- Close calls used in combination with other elements
- Call sequences used in various behavioural contexts
- Call sequences in affiliative contexts
- Need of playback studies to test exact function

(Jansen et al to be submitted)

General discussion

- Banded mongoose show vocal flexibility
 - Production
 - Usage



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- First quantification for segmental concatenation in mammal



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- Importance of vocal cues

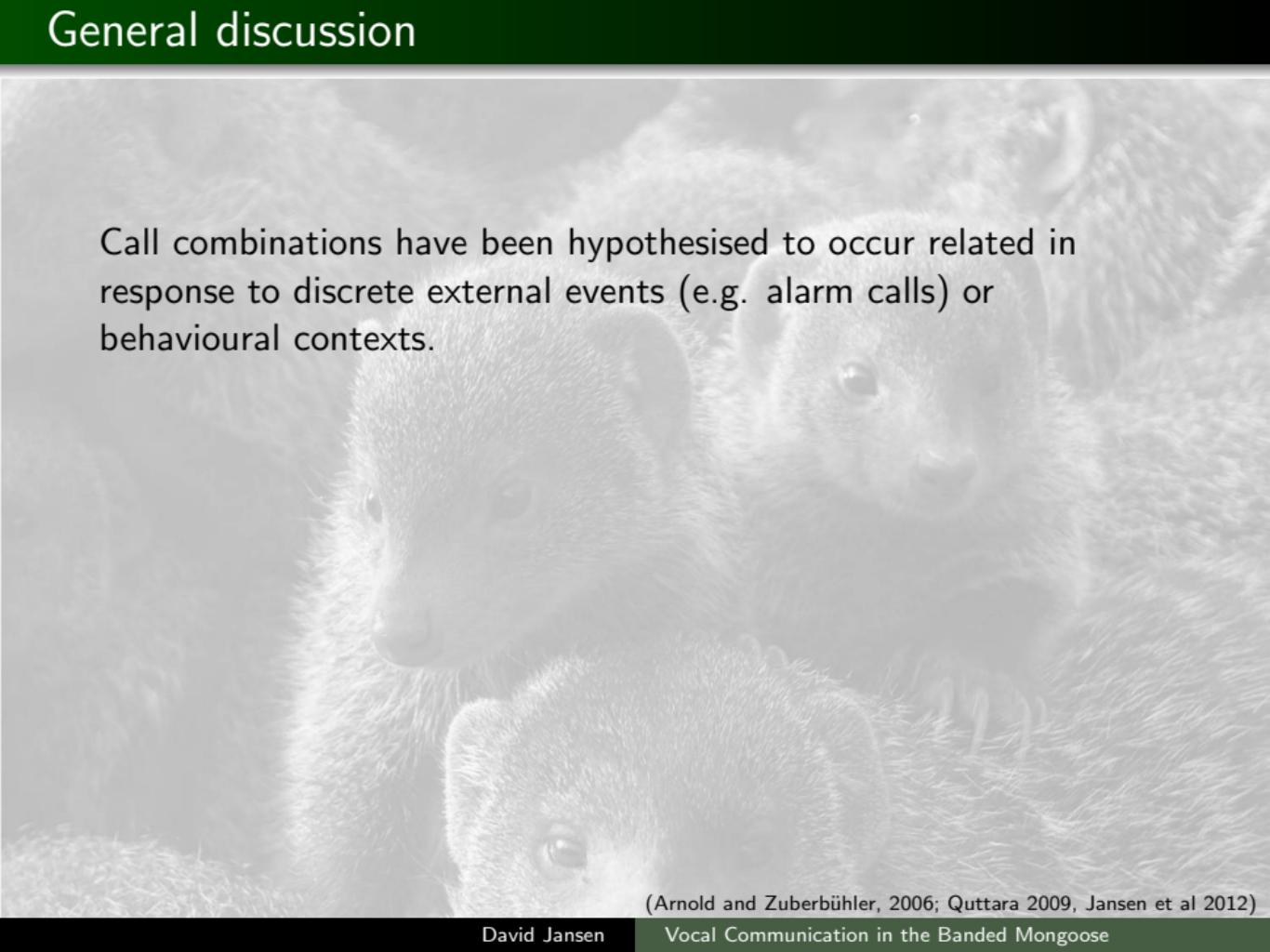


General discussion

- Banded mongoose show vocal flexibility
 - Production
 - Usage
- First quantification for segmental concatenation in mammal
- Importance of vocal cues
- Considerable complexity may lie within a single 'simple' calls



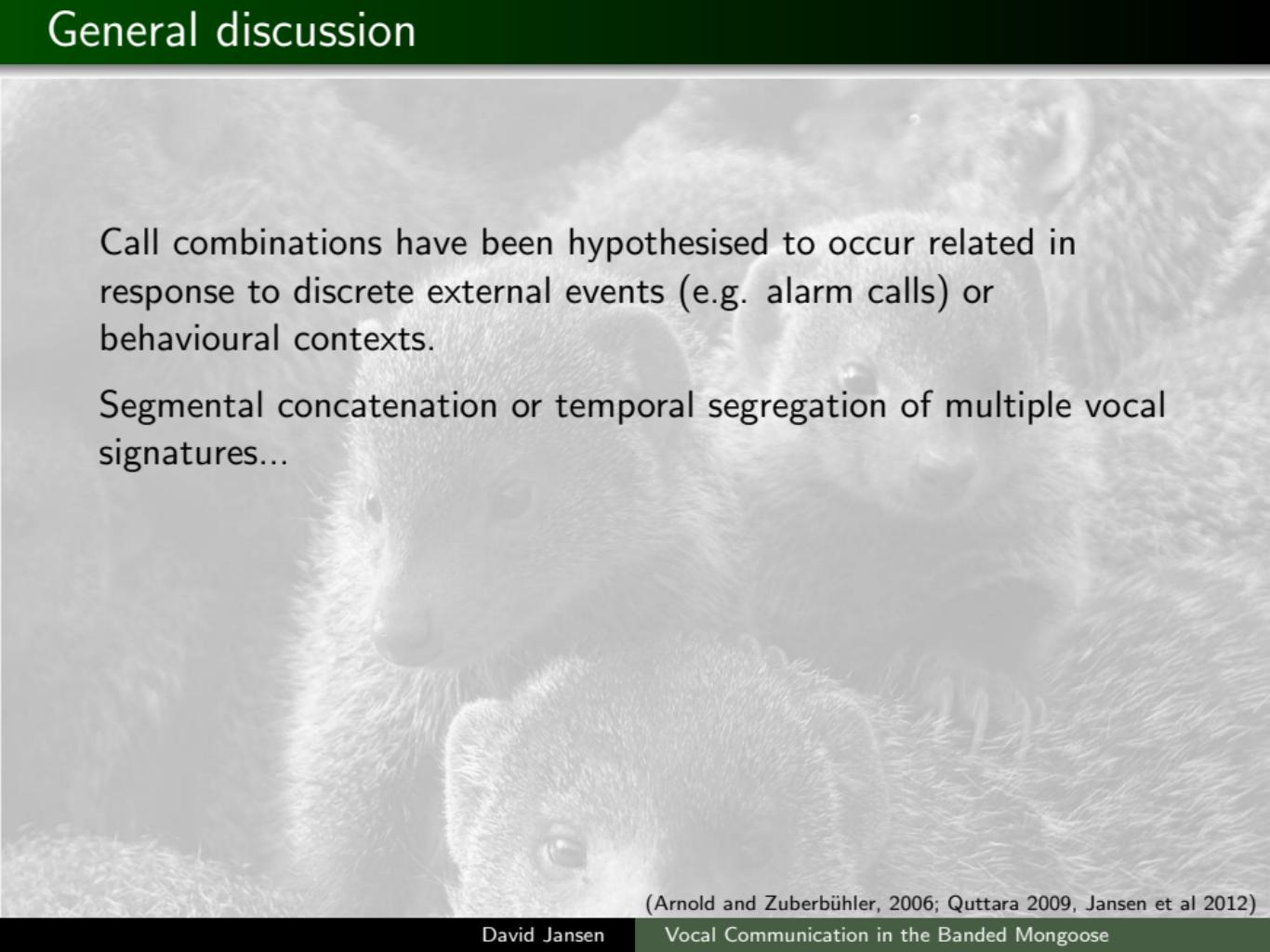
General discussion

A grayscale photograph showing three banded mongooses. One is in the foreground, looking directly at the camera. Behind it are two more mongooses, one slightly above and to the left, and another further back and to the right. They are all facing towards the viewer.

Call combinations have been hypothesised to occur related in response to discrete external events (e.g. alarm calls) or behavioural contexts.

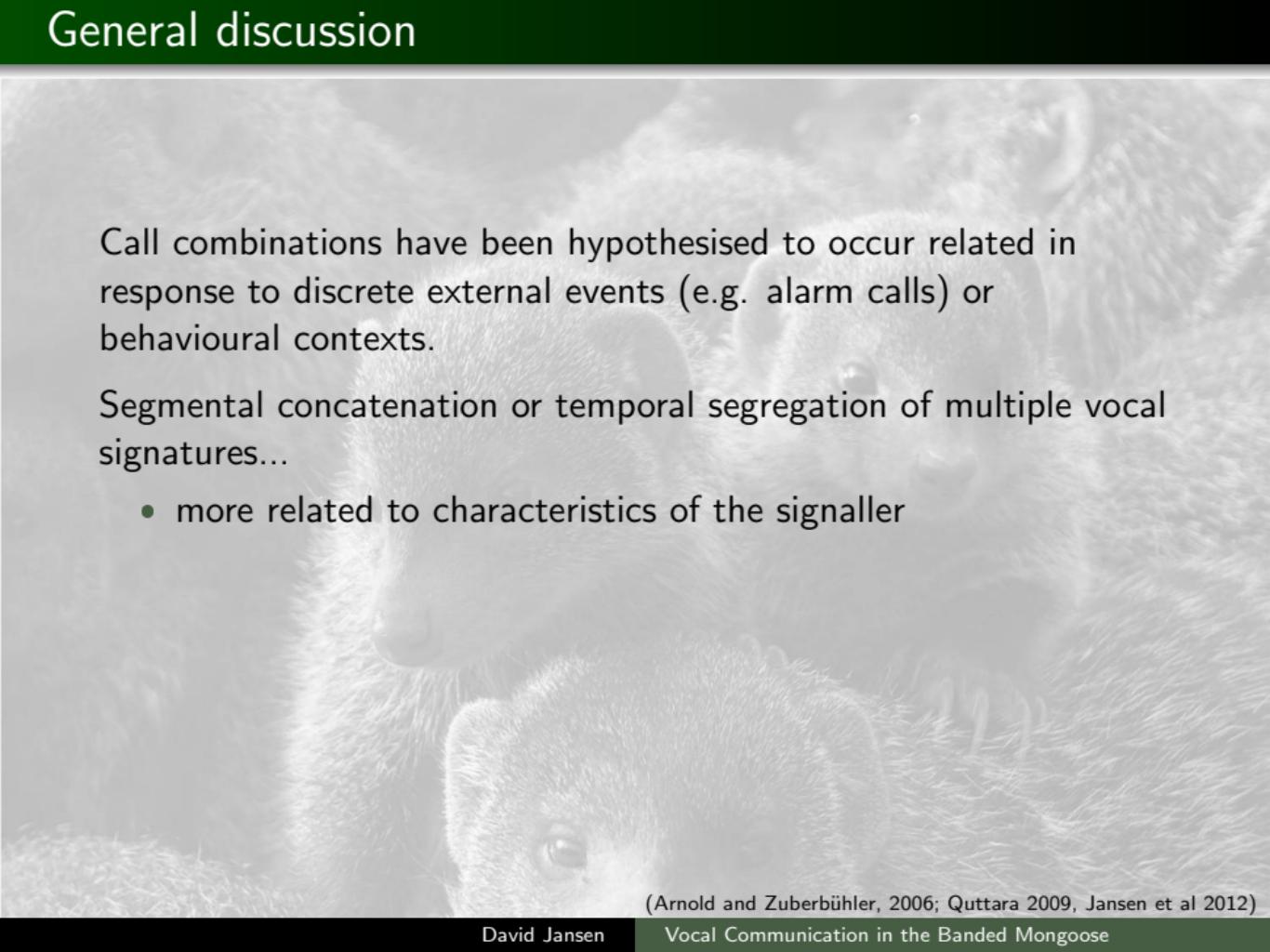
(Arnold and Zuberbühler, 2006; Quttara 2009, Jansen et al 2012)

General discussion



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Segmental concatenation or temporal segregation of multiple vocal signatures...

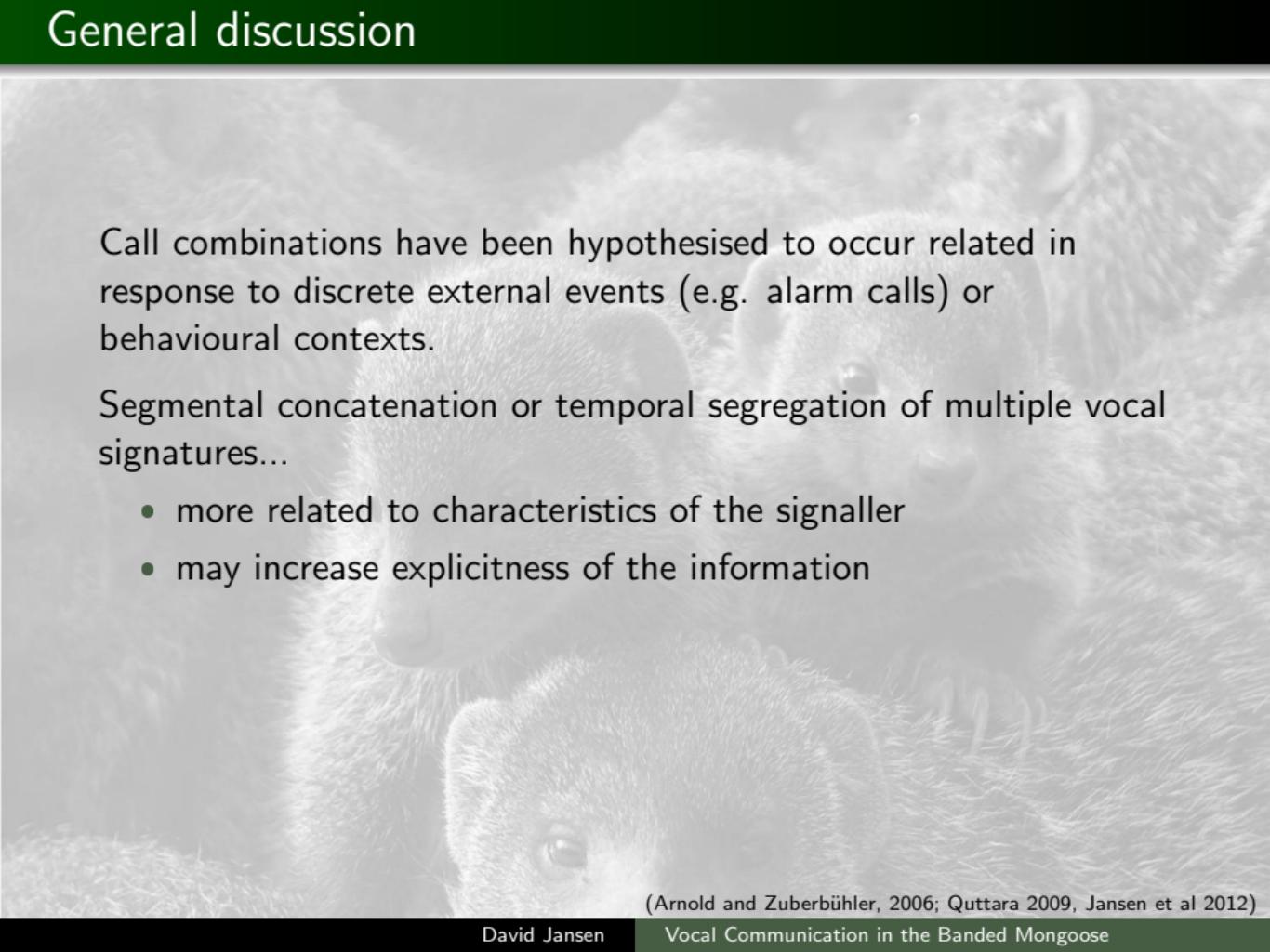


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Segmental concatenation or temporal segregation of multiple vocal signatures...

- more related to characteristics of the signaller

General discussion

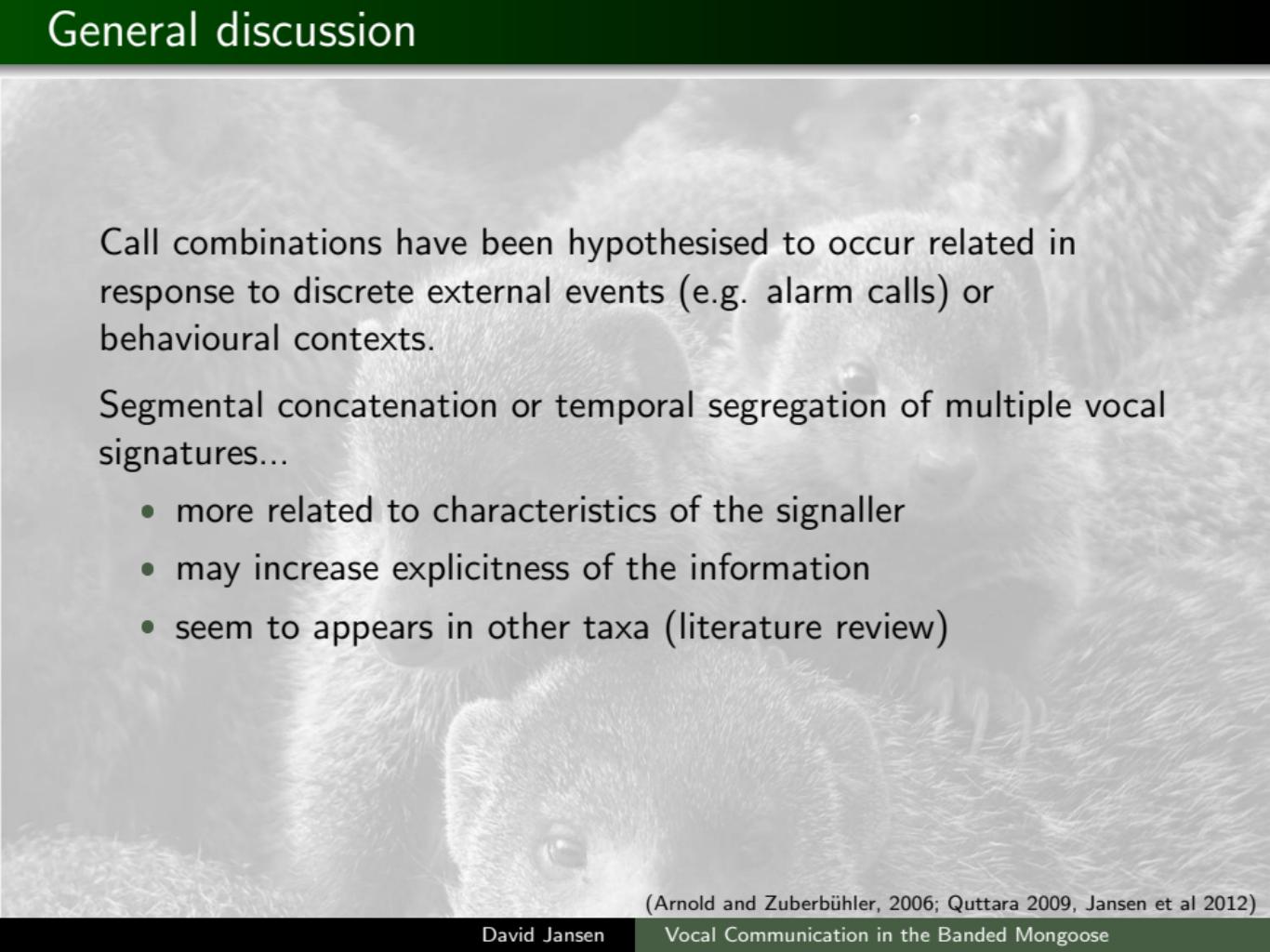


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- may increase explicitness of the information

General discussion

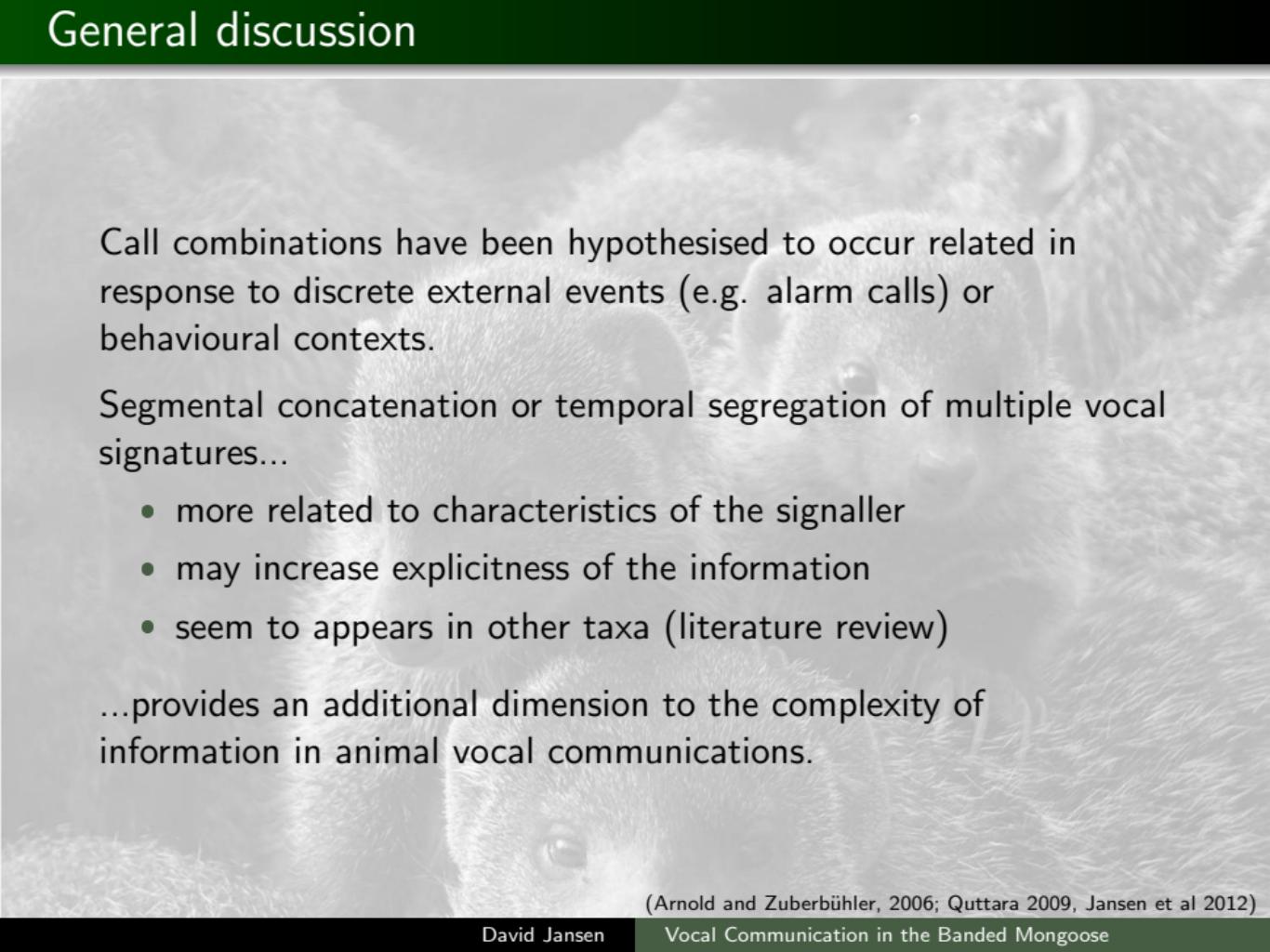


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- seem to appear in other taxa (literature review)

General discussion



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...provides an additional dimension to the complexity of information in animal vocal communications.

Is human language complex?



(Nettle, 2012)

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- Number of discrete 'sounds'
 - 44 phonemes (≈ = sounds) for English language

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But clearly this does not represent the complexity of human language

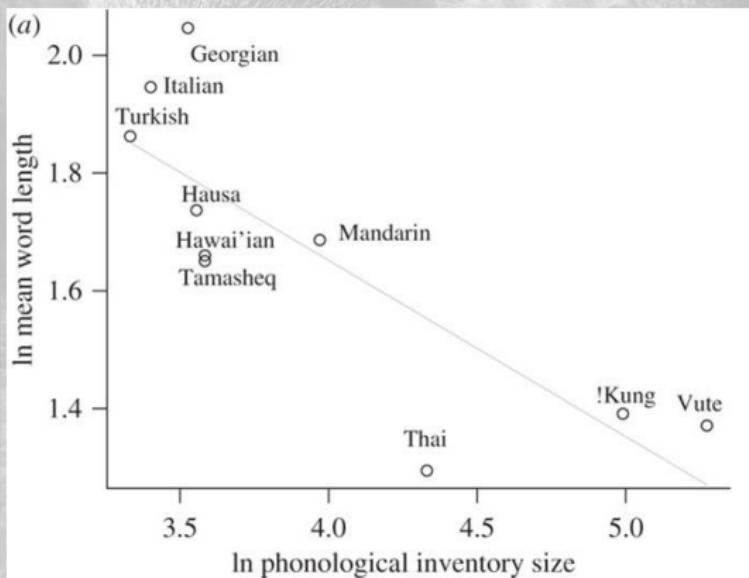
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Is human language complex?

- Number of discrete ‘sounds’
 - 44 phonemes (\approx = sounds) for English language

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- $\approx \frac{1}{4}$ to $\frac{3}{4}$ million words in English language



(Nettle, 2012)

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General discussion



Both call combinations and (temporal separation of) vocal signatures can increase potential quantity of information sets in a species' vocal repertoire.

(Arnold and Zuberbühler, 2006; Quttara 2009, Jansen et al submitted)

General discussion



Both call combinations and (temporal separation of) vocal signatures can increase potential quantity of information sets in a species' vocal repertoire.

⇒ These, and other forms of vocal flexibility, therefore should be considered when comparing species.

Acknowledgements

- Marta Manser
- Mike Cant
- Simon Townsend
- Carel van Schaik
- Funding:
 - University of Zurich (PhD)
 - NERC (long term field site)
- Banded mongoose research project (Exeter University)
- The irreplaceable project field assistants
Francis, Solomon and Kenneth



Questions ???

