

EFFECT OF BEHAVIOURAL CHANGES DUE TO HABITAT DISTURBANCE ON DENSITY ESTIMATION OF RAIN FOREST VERTEBRATES, AS ILLUSTRATED BY GIBBONS (PRIMATES: HYLOBATIDAE)

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SUMMARY

Monitoring programmes often rely on changes in densities of single species to indicate an ecosystem's health. These densities are estimated by a range of census techniques, including line transects and fixed point counts. Using data from gibbons (Primates: Hylobatidae) the present study demonstrates that habitat disturbance (e.g., logging, encroachment) induces changes in the behaviour of species in such a way that it affects density estimation. As a result of disturbance, gibbons alter their response to humans, change their time budgets, and use different canopy levels. Calling rates are generally lowered in response to disturbance and relatively more calls are given at later times of the day. These behavioural changes alter the detectability of gibbons, both positively and negatively. The different factors influencing population estimation act in concert and may be difficult to separate to determine their effect. It is argued that in order to improve the effectiveness of monitoring and censusing, the link between behavioural biology and conservation biology should be strengthened.

INTRODUCTION

Behavioural studies have been considered to be of limited value to conservation because of the discordance in the level of focus between behavioural and conservation biologists. Behavioural research focuses on the level of populations and individuals, whereas many conservation biologists claim that conservation is only effective on higher levels of biological organisation (Clemmons and Buchholz, 1997). Hence, in order to be meaningful, conservation research should focus itself on these higher levels. It may, however, be argued that single species can play an important role in monitoring the health of ecosystems when used as indicators. In order to be useful, indicator(s) should, amongst other things, be amenable, reveal meaningful trends, cost effective to monitor, be consistent, and yield data that are precise and unambiguous in its interpretation (GEC, 1998). Primates may meet some of these demands. They are present throughout the tropics over a large range of habitats, occur often in relatively high densities, and fulfil important roles in their respective ecosystems (Smuts *et al.*, 1987). Hence, primates have been used frequently in monitoring programmes (Glanz, 1982; Brockelman and Ali, 1987; Johns and Skuropa, 1987; Whitesides *et al.*, 1988).

The two most commonly used census techniques to estimate primate densities employed in monitoring programmes or studies to quantify the effects of habitat disturbance are based on line transects (Sen, 1982; Whitesides *et al.*, 1988) and to a lesser extent fixed point counts (Brockelman and Ali, 1987; Brockelman and Srikosamatara, 1993).

The transect technique depends on the detection of animals (or sometimes merely signs such as nests) on one or both sides of a survey path. It has been employed for survey work, where rapid

estimates of populations in inaccessible terrain or in widely different geographic areas are required (e.g., Payne and Davies, 1982; Nijman and van Balen, 1998). It is also used for detailed studies within a limited geographic area, including monitoring of temporal changes in density (Glanz, 1982), for comparisons of habitats within the same general area (Johns and Skuropa, 1987; Blouch, 1997; Johnson and Overdorff, 1999), and for estimation of populations in areas where other methods (mark-recapture, complete counts, home range or territory mapping etc.) are not feasible (Green, 1978; Blouch, 1997). When using the transect method the number of groups detected, the effective sighting distance (an estimate of the distance at which the number of sightings at greater distances equals the number 'missed' at nearer distances) and the group spread (defined as the diameter of a circle of equivalent area to that occupied, on average, by a group of the species under consideration) are parameters needed for estimating densities (Whitesides *et al.*, 1988). For the method to be meaningful, critical assumptions are (i) animals are not affected by the presence of the observer; (ii) groups are always detected on the transect line itself; (iii) groups behave independently.

Censuses based on fixed point counts are widely used in ornithological studies (e.g., Reynolds *et al.*, 1980; Bibby *et al.*, 1992) and are especially suitable in rugged terrain. A similar method has been developed to estimate the density of primates producing loud calls at predictable times of the day, e.g., Indri (Indridae), certain colobines (Colobinae), and gibbons (Hylobatidae) (e.g., Kappeler, 1984; Brockelman and Ali, 1987; Brockelman and Srikosamatara, 1993). This method is based on the number of groups that can be heard calling over a given number of days. The observer is situated at a vantage point and notes the number of groups calling within the census area. This method allows density estimation over relatively large areas in a short time span. In order to calculate densities using fixed point counts, parameters needed include the number of groups calling on a given day, the proportion of groups calling on a given day, and the radius of the area from within songs can be mapped (Brockelman and Srikosamatara, 1993). Critical assumptions include (i) only paired groups call; (ii) groups behave independently; (iii) groups call at least once during the study period.

Johns (1985ab; 1986) followed a primate community in Western Malaysia while their habitat was selectively logged. In his study a number of behavioural changes following logging were observed in a number of species, including: (i) Lar gibbon *Hylobates lar* showed a tendency to increase their freezing behaviour and fleeing noisily decreased; (ii) Activity patterns in *H. lar* and Banded leaf monkey *Presbytis melalophos* changed with a significant increase in time spent resting and a significant decrease in time spent feeding and travelling; (iii) For the same two species there was a significant shift from the upper to the middle canopy level for all types of behaviour combined; (iv) During heavy disturbance, gibbons often ceased calling altogether, and calling rates may have remained depressed for several years after logging had ceased. Similar behavioural changes were found by J. Mitani (*in* Berenstein *et al.*, 1982) when comparing the singing behaviour of Bornean gibbon *H. muelleri* in forest prior and after the drought and fire associated with the 1982-1983 El Nino Southern Oscillation Event. Population numbers remained unchanged, but audible ranges of songs decreased, frequency of singing declined, and gibbons sang from lower heights.

Since these behavioural changes may be relevant to monitoring and censusing, the present study considers two questions: 1. How and to what extent do primates alter their behaviour in response to human induced changes in their environment (e.g., logging, hunting, encroachment), and 2. Do these behavioural changes affect population density estimates when using either the transect method or fixed point counts?

The implications may be crucial when comparing the results of surveys in habitats differing in their degree of disturbance and in monitoring programmes where disturbance levels change over time. Whether behavioural changes do affect density estimation will be illustrated with examples from studies on different gibbon taxa from the Indo-malayan region, but the conclusions and recommendations are most likely to be valid for other regions and for other rain forest vertebrates as well, including other primates, mammals, and birds.

In order to address the two questions, a comparison is made between the behaviour of gibbons in disturbed and undisturbed situations and the subsequent implications for monitoring are assessed. The behavioural changes can both affect the parameters needed for density estimation and violate the (critical) assumptions of the methods employed.

MATERIAL AND METHODS

Gibbons are territorial and live in monogamous family groups consisting of an adult pair with none to four offspring. Gibbons are completely arboreal, and are largely frugivorous. Paired groups give loud morning calls, which can be heard over several kilometres, whereas single individuals rarely call (Leighton, 1987; pers. observ.). The present study concerns data collected on Bornean gibbon *H. muelleri* in East Kalimantan (Kayang Mentarang National Park and adjacent areas in 1996 [115°51'E, 2°50'N]) and Javan gibbon *H. moloch* on Java (Gede-Pangrango National Park and adjacent areas in 1994-1999 [107°00'E, 6°45'S], and Dieng mountains proposed National Park and adjacent areas in 1995-1999 [109°35'E, 7°06'S]).

Undisturbed and disturbed study sites were selected either in close proximity and were similar in climate, original vegetation type, altitude and topography (Gede-Pangrango and Kayang Mentarang), or a forest area was sampled before (1995-1998) and during logging (1999) during the same months of the year (Dieng). Given the close proximity and similarity of the forest areas, it is anticipated that the behaviour of the gibbons prior to the commencement of disturbance did not differ significantly. Sets of disturbed and undisturbed areas had mean densities differing less than 10%, which was established by a number of techniques (line-transects, range mapping, fixed point counts). For the present study, disturbance is taken in a rather broad term and may include hunting, encroachment, small scale logging, commercially (selective) logging, or a combination. Behavioural measurements were collected along line transects, on vantage points during fixed point counts, and ad libitum while surveying in the forest. Singing behaviour of at least eleven *H. moloch* groups was monitored in Dieng for 35 days in Sept-Oct 1998 (pre-logging) and for 25 days in Sept-Oct 1999 (during logging). Some additional data on singing behaviour of Siamang *H. syndactylus* was collected in Way Kambas National Park, Sumatra (1994 and 1999 [105°36'E, 4°50'S]).

For all analyses non-parametric statistics were used (Siegel, 1956) and Yates's correction for continuity was applied in the Chi-sq. tests where appropriate.

RESULTS

1. Behavioural changes affecting line transect censusing

i. Responses to observers

The most common response of gibbons to the approach of a human is to flee. This can be accompanied by branch shaking and vocalising. Alternative responses include freezing, i.e., remaining immobile, and hiding, i.e., moving out of the field of vision of the approacher. Vocalisations are normally uttered only when the primates detected humans at close proximity.

Table 1 Behavioural responses of two gibbons species to an observer in disturbed versus undisturbed habitats. Cases where the gibbons did not detect the observer are excluded.

Species Study site	Fleeing plus vocalising	Fleeing without vocalising	Freezing	Hiding
<i>Hylobates muelleri</i>				
Kayan Mentarang (1)				
undisturbed	20	10	4	1
disturbed	12	8	4	3
<i>Hylobates moloch</i>				
Gede-Pangrango (2)				
undisturbed	12	9	0	0
disturbed	5	5	1	0
Mts Dieng (3)				
undisturbed	60	32	2	1
disturbed	37	24	2	2

1. Undisturbed forest consisted of primary forest in the Nggeng Bio River valley, whereas disturbed forest consisted of 45 year old secondary forest which was situated c. five km south-east in the Bua Alat river valley, East Kalimantan.
2. Undisturbed situation consisted of relatively undisturbed forest in Gede-Pangrango National Park, whereas the disturbed situation consisted of adjacent (smaller) forest patches outside the park boundaries
3. Undisturbed situation consisted of old secondary forest near Linggo, Central Java, in 1998, whereas the disturbed situation consisted of the same forest area in 1999, when a small scale illegal logging operation was in force.

In response to the continued or the increased presence of humans, gibbons alter their behaviour (Table 1). Freezing and hiding and silently moving away becomes more common, though none of the differences are significant (Chi sq., all $p > 0.05$). In all three study areas, and for both species, the response was in the same direction, i.e. gibbons tended to behave in such a way as to reduce the likelihood of being detected. Increase in freezing, hiding and silently moving away, makes it more difficult to locate or detect groups of primates and will lead to a decrease of groups detected. It is furthermore likely that group sizes will be under-estimated as it becomes more difficult to detect all individuals in a group.

ii. *Change in activity patterns*

Primates are most often detected when engaged in conspicuous activities such as vocalising, travelling or feeding, either due to visual or auditory cues of the animals themselves or their surroundings (moving of branches, falling fruit etc.). They are less easily detected when resting. Since time spent travelling and feeding is lowered in disturbed forests, this means that fewer groups will be detected in disturbed habitats. This will also include groups at the transect line, violating one of the critical assumptions of the method. Considered in isolation, the observed change in activity patterns will lead to an under-estimation of true densities in disturbed habitats.

iii. *Use of canopy levels*

Gibbons prefer tall trees for certain activities. Emergent trees and the upper canopy are disproportionately used (favoured) for singing and travelling (cf. Kappeler, 1984; Johns, 1986). In disturbed forests, due to the loss of many large trees, generally activities have shifted from the

upper to the middle canopy (Figure 1: *H. lar*: Chi sq. = 89.4, df=3, $p < 0.01$; *H. moloch*: Chi sq. = 6.10, df=2, $p < 0.05$, middle and lower canopy pooled). Since detection probability decreases with increasing distance between the observer and the animal, primates are more easily detected at lower canopy levels. In general, the shift to lower forest strata will lead to an increase of groups detected.

Figure 1 Percentage of canopy use by two gibbon species in disturbed and undisturbed habitats

2. Behavioural changes affecting fixed point counts censusing

i. Calling rates

The frequency of calling in gibbons is dependent on, among other things, population density, weather (rain, wind), and seasonality of food production (e.g., Chivers and Raemaekers, 1980; Brockelman and Ali, 1987; V. Nijman, unpubl. data). Disturbance in the form of for instance logging will lead to an increase in ambient temperature in the forest, greater differences in temperature between day and night, and an increase in windiness (e.g., Grieser-Johns, 1997). These changes in the (micro)-climate of the forest can affect calling rates.

Contrary to one of the critical assumptions of the fixed point count method, groups do not behave independently. In the present study it was found that songs were stimulated by neighbours (*H. moloch* and *H. muelleri*), and sometimes songs seemed to pass round the local population (*H. moloch*, *H. muelleri*, and *H. syndactylus*). Lowered calling activity makes detection less likely, whereas estimation of the proportion of groups calling on a given day becomes more prone to errors.

ii. Distribution of calls

During a study into an undisturbed population of *H. moloch*, Geissmann and Nijman (in press) noted that some 85% of the female calls and all male calls were given within four hours after sunrise. In disturbed situations, timing of calling changes, with more groups calling later during the day (Table 2). As air heats up during the day locating groups becomes more difficult and the estimation of distance between the observer and gibbons becomes more error prone (cf. D.J. Chivers in Duckworth *et al.*, 1995). Lowered precision in locating groups may result in two groups calling from the same general direction being recorded as one, whereas the estimation of

the radius at which songs can be mapped becomes more difficult. This in effect can influence density estimation in either a positive or negative direction.

Table 2 Number of days *Hylobates moloch* groups were heard calling at different times of the day (Mts Dieng 1998-1999).

Habitat	Time after sunrise (hrs)	
	<6	>6
Undisturbed	34	1
Disturbed	19	6

Fisher Exact probability test, $p < 0.01$

DISCUSSION

The data indicate that gibbons (and probably other primates as well) do respond differently to the presence of humans, including surveyors, in disturbed habitats than in undisturbed habitats (cf. Johns, 1985a; 1986). In the present study, hunting levels were generally low, but high hunting pressure can alter the behaviour of primates to an even greater extent (Kavanagh, 1980; Watanabe, 1981). When conducting line transects, fewer groups will be detected in disturbed habitats as gibbons show an increase in freezing, hiding, and silently moving away. A decrease in conspicuous activities such as vocalising, travelling and eating, as reported by Johns (1985a; 1986), should lead to a decrease in number of groups observed, and may violate the assumption that all groups are detected on the transect line. Only if the decrease in number of groups is unequal for groups on the transect line and groups located farther away, in such a way that groups on the transect line are still always recorded, a decrease in groups detected will not necessarily result in a reduction of estimated density (Skorupa, 1987). However, as there is no indication whatsoever that the number of groups detected on the transect line itself will not have decreased, one of the critical assumption of the line transect method is violated. This will lead to an under-estimation of true densities. Under-estimation of true densities will be even stronger when indeed actual group sizes are under-estimated owing to the increased difficulty in counting individuals. However, not all behavioural changes by gibbons will lead to an under-estimation of true densities, since the marked increase in the use of the lower to middle canopy over the upper canopy in disturbed habitats makes it easier for an observer to detect gibbons.

Calling frequency in gibbons is dependent on a number of environmental variables, including population density, weather, temperature in the forest, and seasonality of food production (Chivers, 1974; Kappeler, 1984; Brockelman and Srikosamatara 1993; V. Nijman unpubl. data), which all might be affected by habitat disturbance. Logging will induce changes in the micro-climate of the forest including an increase in ambient temperature, greater differences in temperature between day and night, and an increase in windiness (e.g., Grieser-Johns, 1997). Habitat disturbance may also alter the acoustical environment on which organisms rely for communication (Clemmons and Buchholz, 1997). Increase in windiness will lead to a significant decrease in calling (*H. pileatus*: Brockelman and Srikosamatara, 1993), and changes in the ambient temperature may affect pre-dawn calling by males in two species (*H. klossi* and *H. moloch*), as pre-dawn calling in male Kloss' gibbons is positively related to temperature (Whitten, 1982).

Contrary to one of the critical assumptions of the fixed point count method, groups do not behave independently. Songs were stimulated by neighbours (cf. *H. lar*, Raemaekers and Raemaekers, 1985), and songs seemed to pass round the local population as has been reported in other studies (Brockelman and Ali, 1987). Fixed point counts are furthermore affected by a depression of calling rates during the day, and possibly by an increase in pre-dawn calling. Lower calling rates make detection less likely, and calls given later during the day makes distance estimation more difficult.

Similar to the studies conducted by Johns (1985ab; 1986) and J. Mitani (*in Berenstein et al.*, 1986), the present study compared the behaviour of primates in areas where the true density was either very similar or had remained virtually the same. Effects of a lowered (or increased) density were not taken into consideration. Habitat disturbance often has an effect on density, due to a lowered carrying capacity of the forest, lowered fecundity, higher mortality (aggravated by an increase in hunting), and sometimes due to groups migrating out or into an area. Lowered densities will introduce additional changes in the parameters needed for density estimation, including smaller group spread for smaller groups, smaller effective sighting distance due to reduced group sizes (e.g., van Schaik *et al.*, 1983; V. Nijman unpubl. data), and a disproportionate reduction of calling rates (V. Nijman, unpubl. data). Alternatively, locally habitat disturbance may lead to larger group sizes and higher densities. In degraded forest with a discontinuous canopy the obligate arboreal nature of many primates, and gibbons in particular, does not permit them to move from one remnant forest patch to another. This induces delayed dispersal of sub-adults, leading to larger group sizes and (temporarily) higher densities (e.g. Brockelmann *et al.* 1998; Oka *et al.* 2000).

Comparing census data from habitats differing in degree of disturbance should be viewed with caution and conclusions should be drawn with care. The mere observation that certain animals are more/less often recorded in these different habitats in itself carries little information. Hence, comparisons of abundances of vertebrates in disturbed and undisturbed situations based on encounter rates only, as done extensively for example by Grieser-Johns (1997) when reviewing the responses of vertebrates in relation to timber production and biodiversity conservation in tropical rain forests, becomes in effect meaningless.

CONCLUSION

Habitat disturbance clearly alters the behaviour of gibbons, and probably many other vertebrates, in such a way that it affects density estimation. Behavioural alterations may be species specific, but may also be related to the types of disturbance, such as the presence or absence of hunting / capturing. Different factors influencing population size estimation act in concert, and may be very difficult to separate to determine their net effect. When comparing census data from habitats differing in their degree of disturbance, the effect of behavioural alterations should be recognised and conclusions drawn with care. It is concluded that there is an increased need for understanding the behavioural plasticity of indicator species, and behavioural studies should play a more prominent role in conservation. Strengthening the link between studies in behavioural biology and conservation biology is needed for improved monitoring and censusing (cf. Beissinger, 1997; Clemmons and Buchholz, 1997).

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