NONRANDOM MOVEMENT BEHAVIOR AT HABITAT BOUNDARIES IN TWO BUTTERFLY SPECIES: IMPLICATIONS FOR DISPERSAL

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Abstract. We observed meadow brown (Maniola jurtina) and gatekeeper (Pyronia tithonus) butterflies at habitat boundaries and observed spontaneous movements out of suitable habitat in order to investigate such movements in relation to dispersal. We found that butterflies of both species were aware of the position of a highly permeable habitat boundary without needing to cross it. Nevertheless, a considerable proportion of butterflies close to the boundary left their habitat (25–43%). Butterflies that crossed the boundary, and moved substantial distances into unsuitable habitat (up to 350 m in M. jurtina and 70 m in P. tithonus), usually returned to their original habitat patch (98–100%). Movement trajectories, at least in M. jurtina, were significantly different from, and more directed and systematic than, a correlated random walk. Approximately 70–80% of spontaneous movements into unsuitable habitat in both species were “foray” loops comparable to those described in mammals and birds. We conclude that, since migrants seemed to have considerable control over leaving their patch and over their subsequent movement trajectories, chance encounter rates with habitat boundaries, and indeed habitat leaving rates, might be less crucial in determining dispersal rates than is usually assumed. In addition, random dispersal trajectories should not be taken for granted in population or evolution models.

Key words: correlated random walks; dispersal trajectories; emigration; habitat edges; habitat fragmentation; movement behavior; navigation; orientation; search strategies; search trajectories.

INTRODUCTION

Dispersion has crucial implications for the dynamics and persistence of populations, the distribution and abundance of species, community structure, gene flow between populations, local adaptation, speciation, and the evolution of life-history traits, especially in fragmented landscapes (see Hanski [1998], Travis and Dytham [1998], and Dieckmann et al. [1999] for reviews). In fragmented landscapes, animal dispersal consists of two component behaviors (e.g., Matthysen 2002): (i) emigration out of an original habitat patch and (ii) subsequent search for a new habitat patch. With respect to the first, it has been assumed that emigration rates out of habitat patches depend on the chance rate of encounter with habitat boundaries (Haddad 1999, Golden and Christ 2000). This assumption is important from a theoretical point of view because it has been used to predict emigration rates based on circumference:area ratios of habitat patches (see Hanski 1998 for a review). It is also practically important because it implies that modification of the ratio of habitat edge to area could be used as a conservation measure to influence emigration rates (Stamps et al. 1987, Ries and Debinski 2001). With respect to the second component of dispersal, it is usually assumed that dispersers search for new habitat in the manner of a correlated random walk (e.g., Hanski 1998, Travis and Dytham 1998, Dieckmann et al. 1999, Armworth et al. 2001, Byers 2001). Again this assumption is crucial, since it leaves individual dispersers only a very limited scope for controlling dispersal rates and directions (Zollner and Lima 1999). Additionally, dispersal distances, dispersal success, and dispersal mortality depend largely on the search strategy that individuals employ once they have left their original habitat patch (Conradt et al. 2003, Leon-Cortes et al. 2003, Doerr and Doerr 2005).

Notwithstanding the widespread use of assumptions such as these in theoretical ecology, empirical information about dispersal is scarce and often only indirect, relying usually on behavioral observations conducted solely at habitat boundaries or on mark–release–recapture (MRR) data (see Schultz and Crone [2001] for a comparison between emigration rates predicted by boundary responses and MRR data and Kindlmann et al. [2004] for a comparison of empirical MRR data and simulation results based on different assumptions of movement rules; see also Haddad [1999], Matthysen [2002], Schooley and Wiens [2004], Doerr and Doerr [2005] for the importance of detailed movement paths). As regards emigration, for example, it is seldom known whether individuals that leave habitat patches are genuine emigrants, since their subsequent destination is not recorded. Hence, they might return to their original habitat patch rather than settling in a new one (e.g., Roper et al. 2003). If individuals recognize habitat
boundaries easily and/or return at a high rate once they have left their original habitat patch, they would have a substantial degree of control over the decision to emigrate, so that chance encounter rates with habitat edges and circumference:area ratios could be poor predictors of emigration rates (e.g., Matthysen 2002). As regards the search strategy of dispersers, several alternatives to correlated random walk are possible (Bell 1983, Zollner and Lima 1999, Doerr and Doerr 2005) and empirical evidence suggests systematic rather than random search in at least some species (Conradt et al. 2000, 2001, Doncaster et al. 2003, Roper et al. 2003, Seymour et al. 2003, Kindlmann et al. 2004, Doerr and Doerr 2005).

Here, we report the behavior of meadow brown butterflies, Maniola jurtina, and gatekeeper butterflies, Pyronia tithonus, at habitat boundaries that posed no physical obstacles to emigration (i.e., highly permeable boundaries; Collinge and Palmer [2002]). We used two butterflies as model species because theoretical development in metapopulation ecology is based on a considerable degree on butterfly systems (see Hanski [1998] for a review). We followed every spontaneous movement from suitable habitat across unsuitable habitat and back to suitable habitat. We aimed to determine (i) whether butterflies recognize habitat boundaries; (ii) whether butterflies that cross habitat boundaries and leave a habitat patch are always genuine emigrants/dispersers, or whether they sometimes return to their habitat patch; and (iii) whether butterflies fly in the manner of a correlated random walk across unsuitable habitat or use forms of systematic search.

METHODS

Study site

The study site was in Stammer Park, Brighton, UK. Butterflies were observed at the boundary of a 190 m long, 10–40 m wide patch of long grassland (Fig. 1). This patch was L shaped, consisting of a “short leg” (80 m, facing east) and a “long leg” (110 m, facing south). Both legs were bordered along one side by a high hedge or woodland and on the other side by a large area of regularly mown, short grassland. The linear extension of both legs consisted of hedges or woodland. Other patches of long grassland occurred at distances of at least 120 m from the observation patch.

Study species and habitat

Maniola jurtina and Pyronia tithonus are both common British butterflies. Their larvae feed on grassland species, and long grassland verges are their natural habitat (e.g., Brakefield 1982). Therefore, we refer to long grassland as “habitat,” whereas habitats unsuitable for the species (e.g., shrubs, hedges, woodland and short grassland; Conradt et al. [2000]) are termed “nonhabitat.” The edge between habitat and nonhabitat is termed the “boundary.” Since the boundary between long and short grassland in the present study did not pose physical obstacles for butterflies with respect to leaving the habitat patch, it was considered as potentially highly permeable (relative to other typical habitat boundaries which the species encounters naturally, such as hedges and forest boundaries; Brakefield [1982], Buechner [1989], Fagan et al. [1999], Ries and Debinski [2001]; see Fig. 1).

Data collection

Data were collected in July and August 2003 (M. jurtina and P. tithonus) and 2004 (M. jurtina). Observations consisted of patrolling the habitat boundary from the side where it was bordered by short grassland. Every butterfly seen within 5 m of either side of the boundary was followed until it either moved further than 5 m into habitat (in the same patch or in another patch), was prematurely lost from sight, or moved further than 350 m (since the logistics to follow further proved insurmountable). Altogether, 396 M. jurtina and 175 P. tithonus were observed of which only one M. jurtina was lost from sight and one M. jurtina moved further than 350 m (and was assumed to have dispersed). Since data collection had to be opportunistic, butterflies could not be marked. However, large population sizes (estimates according to typical densities: about 430 M. jurtina and 210 P. tithonus; Conradt et al. [2001]), combined with the short lifespan/residence times of individual butterflies (e.g., median life span is 7 d in M. jurtina; Conradt et al. [2001]) relative to the observation periods, made it unlikely that pseudo-replications would be problematic. For example, we...
estimated that the probability not to have a single individual replication in the sample of flight paths for *M. jurtina* was 95% in 2003 and 99% in 2004; and 97% for *P. tithonus* in 2003 (assuming a similar life span for *P. tithonus* as that reported for *M. jurtina*).

Data on most flight paths were collected in a relatively simple manner for three reasons: first, because we were largely interested in quantitative rather than qualitative aspects of behavior; second, in order to achieve sufficiently large sample sizes; and third, so as not to bias observations toward shorter flights that were likely to be mapped in detail more completely than longer flights. Therefore, the majority of flight paths were recorded in the following manner. Markers were dropped at the place where a butterfly (i) was first seen in habitat; (ii) left its original habitat patch; (iii) returned to habitat (whether into the same patch or another); or (iv) where the observation was terminated. Where applicable, markers were also dropped at the furthest distance that the butterfly reached from its original habitat patch (for example, for a loop-like trajectory, this would be the turning point of the loop). Where butterflies were lost, a marker was dropped at the point of loss.

Additionally, 34 flights of *M. jurtina* were mapped in more detail. Since butterflies flew in stretches of almost straight movements with distinct recurrent turnings, each straight stretch was defined as a move (as recommended by Turchin [1998:128], in order to avoid the problems of over- or undersampling of paths). We dropped markers at the end of every move and measured move lengths and turning angles. Observed flight lengths ranged from three to 30 moves. Altogether, a pooled sample of 461 turning angles and 495 move lengths was collected. Only flights which started in habitat and went into nonhabitat were used, before the start of the flight it was decided whether the flight would be mapped in more detail and such detailed flight data were collected throughout the field season, so that these 34 flights represent a random sample of flights into nonhabitat.

**Habitat use and behavior at habitat boundaries**

We noted (i) whether a butterfly was first seen in habitat or nonhabitat; and (ii) whether it crossed the boundary.

**Movement behavior in nonhabitat**

**Distances moved from habitat and return to habitat.**—For flights marked using the “simple” method, we measured by pacing the maximum orthogonal distance which a butterfly moved away from its original habitat boundary before it returned, got lost, or migrated into a new patch (maximum distance moved from habitat; Fig. 1). Note that this is not necessarily the distance between furthest turning point/point at loss and habitat leaving point, but the most direct distance to the habitat boundary. Pacing was calibrated in meters and always done by the same observer (L. Conrart). Where the analysis was based on the number of butterflies that flew at least to a given distance, lost butterflies could be included if their point of loss was above the maximum distance used in the analysis (losses were small). We also noted, if a butterfly moved into nonhabitat, whether it returned to the observation patch or a new patch.

**Movement trajectories.**—

1. **Mean net squared displacement.**—For 34 flight paths of *M. jurtina* that were mapped in detail, the observed mean net squared displacements were calculated for numbers of moves from one through 30 (i.e., the mean over all flights of the squared distance between the butterfly’s starting point and position after a given number of moves; Turchin [1998]). Those mean net squared displacements (for given numbers of moves) were compared to the respective predicted mean net squared displacements for a correlated random walk derived by a bootstrapping method (Turchin 1998), as follows. First, 15 000 pseudopaths (based on a correlated random walk; Turchin [1998]) were simulated by drawing turning angles and move lengths randomly from our pooled sample of observed turning angles and move lengths \((f = 461 \text{ observed number of turning angles, } m = 494 \text{ observed number of move lengths})\). For these simulated 15 000 pseudopaths, the simulated net squared displacement and the variance in simulated net squared displacement were calculated for each path length of 1–30 moves. The average simulated net squared displacement of all 15 000 simulations is the predicted net squared displacement for each given path length for a correlated random walk. The distribution of the predicted mean net squared displacement over \(n\) simulated flights for a given path length can then be approximated by a normal distribution with predicted net squared displacement as mean and variance in simulated net squared displacement divided by \(n\) as variance (Zar 1984). From these normal distributions, 95% confidence intervals were calculated for the predicted mean net squared displacement for each given path length, using the observed sample sizes at each path length as \(n\) (note that \(n\) varies for different path lengths, because not all observed paths reached the maximum length of 30 moves). If observed mean net squared displacements lay outside this 95% confidence interval for the predicted mean net squared displacement, observed paths differed significantly (with \(P < 0.05\)) from the predictions of a correlated random walk. Observed mean net squared displacements significantly larger than the predicted mean net squared displacements indicate that observed paths are more directed than expected by a correlated random walk. Observed mean net squared displacements significantly smaller than the predicted mean net squared displacements indicate that observed paths are less directed and more winding than predicted by a correlated random
walk (see also Turchin [1998] for a very detailed description of this method).

In addition, we investigated whether observed turning angles were autocorrelated (Turchin 1998) by examining whether consecutive turning angles tended to be less often to the same direction (either right or left) than expected by chance (i.e., whether there was a first-order negative autocorrelation), and whether once-removed-consecutive turning angles tended to be more often to the same direction than expected by chance (i.e., whether there was a second-order positive autocorrelation). For this purpose, we counted the observed number of turns in the same direction (i.e., number of occasions left turn follows on left turn plus number of occasions right turn follows on right turn: “left-left” turns plus “right-right” turns), and the observed number of turns in opposite direction (i.e., “left-right” plus “right-left” turns). We calculated the relevant expected numbers assuming independence of turning directions (approximately 50% of turns were left, 50% right; thus the probability of observing left-left turns was 25%, right-right turns 25%, left-right turns 25%, and right-left turns 25%) and compared expected and observed numbers using $\chi^2$ tests. A significantly larger number of observed than expected turns in the same direction means positive autocorrelation of turning angles. A significantly larger number of observed than expected turns in the opposite direction means negative autocorrelation of turning angles (see also Turchin [1998] for a detailed description of the method). A first-order negative together with a second-order positive autocorrelation of turning angles indicates (i) that paths are not correlated random walks; but (ii) that previous directional changes are compensated for nonrandomly by following a zigzag trajectory.

2. Self-crossing of paths and qualitative categorization of movement trajectories.—In addition, the flight trajectories were categorized qualitatively by sight with respect to (i) whether they crossed themselves; and (ii) whether they consisted of loop-like movements (involving leaving the habitat and then returning in a half-circle or half-elliptic “loop” back to habitat; see Fig. 1). Only movements $>5$ m into nonhabitat were included in this analysis. Such loop-like movements would be expected if butterflies used a foray search strategy for dispersal (Durier and Rivault 1999, Conradt et al. 2000, 2001). Both these qualitative assessments were easy in the field because of the high visibility in short grassland, the manner of observations (the observer followed the route of the butterfly from a reasonable distance; Conradt et al. [2000]), and not least the very unambiguous nature of the flights themselves. To calculate the expected frequencies of (i) self-crossing and (ii) foray-looping flights, pseudopaths based on correlated random walks were simulated, as described above, for $M. jurtina$, and assessed visually. These simulated paths were terminated in the same manner as the paths with which they were compared, namely when they (i) either returned to habitat; or (ii) exceeded a distance of $150$ m from their original habitat patch (since none of the observed flights got lost until they reached at least a distance of $150$ m).

Results

Habitat use

In both species, significantly more butterflies were first detected<$5$ m inside the boundary (i.e., in habitat) than were detected<$5$ m outside of the boundary (i.e., in nonhabitat). This supports our classification of the study area into habitat and nonhabitat ($M. jurtina$, $330$ in habitat, $32$ in nonhabitat, $\chi^2 = 245.3$, $P < 0.0001$; $P. tithonus$, $167$ in habitat, eight in nonhabitat, $\chi^2 = 144.5$, $P < 0.0001$).

Behavior at habitat boundary

In both species, butterflies first observed<$5$ m inside the habitat boundary were significantly more likely to move deeper into habitat (without previously crossing the boundary) than out of habitat ($M. jurtina$, $187$ moved deeper into habitat, $143$ out of habitat, $\chi^2 = 5.9$, $P = 0.01$; $P. tithonus$, $126$ moved deeper into habitat, $41$ out of habitat, $\chi^2 = 43.3$, $P < 0.0001$). Thus, butterflies seemed to recognize the boundary between habitat and nonhabitat before crossing it. Nevertheless, a considerable proportion of butterflies left the habitat patch at least temporarily (43.4% in $M. jurtina$ and 24.6% in $P. tithonus$), and more so in $M. jurtina$ than in $P. tithonus$ ($\chi^2$ test for difference between species, $\chi^2 = 17.0$, $P < 0.0001$).

Movement behavior in nonhabitat

Distances moved from habitat and return to habitat.—In $M. jurtina$ 43% of butterflies moved up to $160$ m, and in $P. tithonus$ 25% of butterflies up to $70$ m, away from their original habitat patch into nonhabitat (Fig. 2a and b). In $M. jurtina$, only 2.1% (i.e., three) of movements out of habitat resulted in dispersal to different habitat patches, while 97.9% (i.e., 139) of movements ended with a return to the same habitat patch ($n = 142$). Return rates to the starting habitat patch were still very high even for butterflies that had moved a considerable distance into nonhabitat (e.g., 70% of $M. jurtina$ that flew further than $50$ m from their habitat patch returned subsequently; Fig. 2c), and $M. jurtina$ that returned to their original patch had flown up to a maximum distance of $150$ m into nonhabitat before returning (compare this to an average dispersal distance for $M. jurtina$ in MRR experiments of 40–70 m in a landscape consisting of a mixture of pastures and agricultural fields; Brakefield [1982]). In $P. tithonus$, all butterflies that left the habitat patch returned to it ($n = 41$), flying up to $70$ m into nonhabitat before returning.

Movement trajectories.—

1. Mean net squared displacement.—The mean net squared displacement of 34 detailed mapped flights by
M. jurtina (see Fig. 3 for examples) lay outside the 95% confidence interval derived by bootstrap simulations of correlated random walks (Turchin 1998) for flight lengths of up to 27 moves (see Fig. 4; above 27 moves sample sizes were very small, and, thus, the 95% confidence interval too broad to allow for meaningful comparisons). Therefore, the observed movement trajectories were significantly different from, and more directed than, correlated random walks. Additionally, turning angles were significantly first-order negatively and second-order positively autocorrelated, suggesting that butterflies compensated for directional changes in subsequent turns in the manner of a zigzag flight (number of first-order left-left plus right-right turns, 126 observed, 213.7 predicted; number of first-order left-right plus right-left turns, 301 observed, 213.3 predicted; $\chi^2 = 72.0, P \ll 0.0001$; number of second-order left-left plus right-right turns, 230 observed, 196.8 predicted; number of second-order left-right plus right-left turns, 163 observed, 196.2 predicted, $\chi^2 = 11.2, P < 0.001$).

2. Self-crossing of paths.—One of 177 observed flight trajectories by M. jurtina, and none of 41 observed flight trajectories by P. tithonus crossed their own flight path. In contrast, in 250 simulated pseudopaths (in the manner of correlated random walks) for M. jurtina, 93 (37.2%) trajectories crossed their

![Fig. 2. Numbers of (a) Maniola jurtina and (b) Pyronia tithonus that flew to a given distance or farther into nonhabitat (for reasons of clarity, scale is logarithmic); and (c) proportion of M. jurtina that returned to their original patch after they had flown to a given distance or farther.](image)

![Fig. 3. Three examples of M. jurtina flight paths that were mapped in greater detail. Note that the scale differs among paths in panels (a)–(c).](image)
own flight path at least once (and usually numerous times). The difference between observed and simulated trajectories of *M. jurtina* with respect to self-crossing was significant (binomial test, *P* < 0.0001), further suggesting that movement trajectories were more systematic and consequently more efficient than correlated random walks.

3. **Qualitative categorization of movement trajectories.**—Fifty-one of 72 (70.8%) *M. jurtina* flight trajectories and 16 of 20 (80%) *P. tithonus* trajectories (that ventured further than 5 m from the boundary into nonhabitat) consisted of loops which could be classified as “foray search trajectories” (i.e., simple, half-oval shaped loops out of, and back to, the habitat patch [Conradt et al. 2000, 2001; see Fig. 1 and Fig. 3a and b]. By comparison, of 100 simulated correlated random walk pseudopaths for *M. jurtina*, 56 (56%) were foray search trajectories. Thus, observed *M. jurtina* paths consisted significantly more often of foray search trajectories than expected from a random correlated walk ($\chi^2 = 6.5, P = 0.01$).

**DISCUSSION**

Butterflies of both species seemed to be aware of a boundary between suitable and unsuitable habitat without needing to cross it. This indicates that butterflies of both species can actively control their rate of boundary crossing, and that butterflies which crossed into unsuitable habitat did so for a purpose, presumably related to dispersal (Conradt et al. 2000). A large proportion of butterflies moved, at least temporarily, out of their habitat patch, and several butterflies moved considerable distances from their original habitat patch relative to their average dispersal distance. These movements differed clearly from the typical, more frequently turning and slower movements within suitable habitat (L. Conradt, unpublished data), further suggesting that the movements into unsuitable habitat were not related to normal food plant search behavior (Conradt et al. 2000, 2001). Most of the movements out of suitable habitat resulted in a return to the same habitat patch, and only a relatively small proportion of butterflies dispersed to a new patch, as has been predicted by “forced dispersal” experiments in *M. jurtina* (Conradt et al. 2000, 2001) and subsequent dispersal models (Conradt et al. 2003). Movement trajectories, at least in *M. jurtina*, differed significantly from those predicted by a correlated random walk. Instead, butterflies moved in a more directed manner across unsuitable habitat, compensated for directional changes in subsequent turns, and were very efficient in the sense that paths almost never crossed themselves. All this implies that the movements out of habitat were related to dispersal rather than to food plant search (Conradt et al. 2000, 2001, 2003), that dispersing butterflies move systematically, and that the rate of habitat return is under active and effective control.

The notion that emigration rates depend on chance encounters with habitat boundaries (and that, therefore, circumference:area ratios are automatically good predictors of emigration rates out of habitat patches) are based on the assumptions that (i) the probability that an individual leaves a patch is proportional to the probability that it encounters a patch boundary; and (ii) once it has left a patch, it returns to the patch only by chance. Both these assumptions do not hold for the observed movements in *M. jurtina* and *P. tithonus*. If individuals, like the butterflies in our study, can recognize boundaries and, thus, have control over their decision to leave, the rate at which they leave a patch will depend mainly on their incentive to leave (e.g., on patch quality, population density, or similar). The rate at which they encounter boundaries will only play a role if habitat patch size is so large that individuals with the aim to emigrate have difficulties to find a boundary (Mathysen 2002). Similarly, if butterflies can actively find their way back to their patch of origin (rather than drift around “randomly” and return only by chance), the rate of emigration will largely depend on their incentive to continue emigration (e.g., on the detectability of new patches, the hostility of the unsuitable habitat, or similar). Therefore, we suggest that movement out of suitable habitat (and subsequent dispersal) is unlikely to increase in a simple way with the encounter rate of habitat boundaries (Haddad 1999, Ries and Debinski 2001, Schultz and Crone 2001), at least in our two study species. Thus, the use of circumference:area ratios of habitat patches in order to predict relative emigration and dispersal rates (e.g., Stamps et al. 1987, Buechner 1989, Hanski 1998) might not be valid, at least not...
generally. Matthysen (2002) made similar observations in Blue and Great Tits. He argued that if boundary encountering rates are crucial, emigration rates should be higher in birds whose natal territory lay close to a habitat boundary. However, he found that this prediction was not supported in his study site, and suggested instead that boundary encounter rates become crucial only when habitat patches are so large that “willing” dispersers cannot easily detect them. Our study suggests further that estimates of dispersal rates from observation of habitat departures can be unreliable if the majority of habitat leavers return.

In a majority of cases of movements into unsuitable habitat, spontaneous foray loops, similar to those described for foray search dispersal (Conradt et al. 2000, 2001, 2003), were observed in both butterfly species. This supports observations previously made in “forced dispersal” experiments (Conradt et al. 2000, 2001). I suggest that *M. jurtina* and *P. tithonus* habitually reconnote the landscape surrounding their habitat patch, presumably as part of dispersal attempts (Conradt et al. 2000). Predispersal explorations have also been described in mammals (Roper et al. 2003, Haughland and Larsen 2004) and birds (Walters et al. 1992, Rivera et al. 1998, Doerr and Doerr 2005). Foray-search dispersal trajectories have important implications for dispersal distances, efficiency, and mortality (Conradt et al. 2003), and need, therefore, to be taken into account by relevant models (Conradt et al. 2003, Kindlmann et al. 2004, Doerr and Doerr 2005, Zoller and Lima 2005).

In conclusion, we suggest that population-level models which are based on the assumption of systematic search (e.g., foray search) by dispersing individuals, rather than correlated random walks, are urgently need ed (Conradt et al. 2000). First approaches have been made by Zoller and Lima (1999), Conradt et al. (2003 and Heinz et al. (2005) using simulation models. Their results suggest that foray-search type pre-dispersal explorations lead to higher average dispersal success and lower average dispersal mortality, but shorter average and maximum dispersal distances in populations (Zoller and Lima 1999, Conradt et al. 2003). They can also result in lower habitat patch connectivity between distant patches, because of increased “competition” for dispersers by neighbouring patches (Heinz et al. 2005).

**Acknowledgments**

We thank the Brighton and Hove Council for permission to work in Stanner Park. Dr. L. Conradt was supported by a Royal Society University Research Fellowship.

**Literature Cited**


