CAN LIFE HISTORIES PREDICT THE EFFECTS OF HABITAT FRAGMENTATION? A META-ANALYSIS WITH TERRESTRIAL MAMMALS

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Abstract. Anthropogenic fragmentation of habitats has been identified as one of the primary drivers of mammalian declines and extinctions. Previous research has implicated five life history traits as being predictive of the impacts of habitat fragmentation on mammalian abundances: potential growth rate, sociality, mass, home range, and niche breadth. In order to systematically test if these five life histories correlated with mammalian abundances across a gradient of habitat fragmentation, we conducted a meta-analysis. We systematically collected data from 68 studies, encompassing 232 mammalian species within 143 genera, 50 families, and 17 orders. We found that mammals with lower growth rates, paternal care of offspring, greater mass, larger home ranges, and increased niche specialization had significantly lower abundances in fragmented habitat. These results could provide land managers and conservationists with a coarse tool for predicting the impacts of habitat fragmentation across a wide taxonomic breadth of terrestrial mammals.
Keywords: *abundance, mixed-effects model, specialists vs. generalists*

Introduction

Humans have fragmented most continuous habitats on the planet, causing large changes in population sizes of many species (Turner, 1996; Ferraz et al., 2003). Anthropogenic fragmentation is the primary cause of mammalian declines and extinctions worldwide (Wilcove et al., 1998; Grelle, 2005), and has increasingly isolated parks and refuges created to protect wildlife (Janzen, 1983; Newmark, 1995). Despite their conservation status, these fragmented habitats frequently support fewer species, and the species that remain often maintain lower densities when compared to contiguous landscapes (Newmark, 1995).

Despite a large body of literature on the effects of fragmentation, it has been difficult to generalize results across studies because the research focus has typically been the *effects* of fragmentation on a species, and not *why* the species is affected by fragmentation (Funk & Mills, 2003; Banks et al., 2007). In other words, most studies addressed *how* a species is affected by fragmentation (for example, changes in demography or population size), and not what aspects of the species life-history caused the species to be vulnerable (e.g. Ceballos & Brown, 1995; Newmark, 1995; Brashares, 2002).

Proactive, strategic conservation necessitates an evidence-based framework that can be used to predict the impact of anthropogenic disturbances. To accurately target conservation efforts, land managers need to know which species are most threatened by anthropogenic fragmentation and why (Doak & Mills, 1994; Turner, 1996). Several life-history traits have been proposed as predictive of the effects of fragmentation across species (e.g. Laurance, 1994; Ganzhorn & Eisenbeiß, 2001; Laurance et al., 2002), but the predictive capacity of these traits have not been systematically tested (Dale et al., 1994; Peters & Herrick, 2004; Banks et al., 2007), or applied systematically to predict impacts and aide management (Ferguson & Larivière, 2002; Funk & Mills, 2003).

To test whether selected life history traits predict mammal responses to fragmentation, we conducted a meta-analysis of all published literature linking fragmentation and mammals (Englund et al., 1999; Gurevitch & Hedges, 1999; Osenberg et al., 1999). Previous research has proposed that the potential growth rate, sociality, mass, home range, and niche breadth may each predict a directional change in mammal abundances due to fragmentation (*Table 1*). To assess whether the use of these life histories in management is warranted, we tested both the validity and strength of each of the following hypotheses.

Potential Growth Rate

Those species that have the greatest potential growth rate may be more capable of compensating for losses of individuals due to fragmentation (Laurance, 1991; Viveiros de Castro & Fernandez, 2004).

Sociality

Social mammals require groups in order to maintain populations or colonize fragments. Thus social mammals may be less likely to colonize a fragment and more prone to local extirpation than solitary species (Lawes et al., 2000; Swihart et al., 2003). Fragmentation can also have a negative effect on social species by reducing group size and therefore restricting fitness enhancing social strategies (Banks et al., 2007).

Mass

Mammals with heavier body mass require more resources. Because fragments provide a lower quantity of resources, mammals with large body masses may negatively correlate with fragmentation (Marquet & Taper, 1998; Cullen et al., 2001; Michalski & Peres, 2007; Okie & Brown, 2009).

Home Range

Wide ranging species are notably absent from small habitat fragments and may be particularly susceptible to habitat loss (Noss et al., 1996; Woodroffe & Ginsberg, 1998; Feeley & Terborgh, 2008). Thus as the home range of a species increases, the size of the fragment needed to support a viable population increases.

Niche Breadth

Specialists and generalists may respond differently to fragmentation. Specialists, compared to generalists, use fewer resources and thus have fewer alternatives when habitats are constricted. Specifically, specialization of diet, denning, and locomotion could predict a mammal's vulnerability to fragmentation (Laurance, 1990; Laurance,

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1994; Swihart et al., 2003; Viveiros de Castro & Fernandez, 2004; Prugh et al., 2008).

Table 1. *List of life histories and the predicted changes in mammal abundances in response to habitat fragmentation.*

life history	effect of fragmentation	citations
low potential growth rate	negative	Laurance (1991) Viveiros de Castro & Fernandez (2004)
highly social	negative	Lawes et al. (2000) Swihart et al. (2003) Banks et al. (2007)
heavy mass	negative	Marquet & Taper (1998) Cullen et al. (2001) Michalski & Peres (2007) Okie & Brown (2009)
wide home range	negative	Noss et al. (1996) Woodroffe & Ginsberg (1998) Feeley & Terborgh (2008)
specialist	negative	Laurance (1990) Laurance (1994) Swihart et al. (2003) Viveiros de Castro & Fernandez (2004) Prugh et al. (2008)

Materials and Methods

Data Acquisition

On January 27th, 2010 we performed a literature search on Web of Science using three separate groups of phrases in order to avoid biases associated with selection criteria (Englund et al., 1999): 1) “fragment” and “mammal” and “patch,” 2) “fragment” and “mammal” and “habitat,” 3) “fragment” and “mammal” and “disturbance.” Because Web of Science detects word-fragments, a search for “fragment” returns all results for “fragmentation” as well. The results from these three groups of phrases were summed for a total of 1101 studies, and each study’s abstract was read. Based upon the abstracts, we read 304 studies in detail (see *Appendix 1* for the PRISMA flow diagram). Studies were selected for inclusion in the database if they assessed the abundances of terrestrial mammals within at least two unaltered fragments of different sizes. If a study had assessed abundances in fragments but did not include either the abundance estimates or fragment size, we contacted the author and requested the information for inclusion in this study. A total of 68 studies (*Appendix 2*) encompassing 232 mammalian species within 143 genera, 50 families, and 17 orders, were included in our meta-analysis.

Effect Statistic

We were interested in predicting shifts in mammalian abundances in response to anthropogenic fragmentation. To assess whether the aforementioned life history traits could predict changes in mammalian abundance, we needed to first quantify the impact

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of fragmentation on abundances in the form of an effect statistic. In the traditional meta-analysis, the effect statistic is calculated as the standardized difference between two treatments (*d* in Hedges & Olkin, 1985) or the correlation coefficient (*r* in Osenberg et al., 1999). However, nearly all the studies collected for this meta-analysis assessed abundances in more than two habitat fragments; many species abundances were estimated in more than one study; and the goal of our research was to measure the magnitude of the effect of fragmentation on abundances; thus we needed an alternative statistic (Osenberg et al., 1997).

To accommodate these data, we used the regression coefficient from linear mixed-effects models as an effect statistic. By regressing the estimated abundances against the habitat fragment size within each species across studies, the resulting regression coefficient indicated both the strength and the direction of the effect for each species. We compared regression coefficients from linear and exponential regressions and found 127 of 203 species showed a better fit with a linear model. Given that the abundances of 85 species were estimated in two or more studies and given the need for one effect statistic per species in order to avoid pseudoreplication (Hurlbert, 1984), we included study as a random predictor with a fixed slope. Since both the fragment size and abundance estimates varied widely within and across studies, we used their respective logarithmic values (Michalski & Peres, 2007). In order to include abundance estimates of continuous forests in the model, we set their values equal to 10,000 ha (Vieira et al., 2009).

The effect statistic for each species is the negative of the regression coefficient ($-\beta_1$) from the following equation:

$$\log(\text{area}) \sim \beta_0 + \beta_1 * \log(\text{abundance}) + (1|\text{study}) \qquad \text{(Eq. 1)}$$

The (1|study) term allowed the various studies to have different intercepts, but also forced all the studies to have the same slope.

Life History Traits

To quantify a mammal's life history traits, we extracted values from encyclopedic references (Emmons & Feer, 1999; Nowak, 1999; Foresman & McGraw, 2001). If we could not find a given value, we searched for primary literature in Web of Science and in the IUCN Red List of Threatened Species (IUCN 2009). We defined potential growth rate as the litter size multiplied by the number of litters per year and then divided the total by generation time (Pianka, 1970). Each species' sociality received an ordinal score of 0 to 4, with asocial species scored as 0, rudimentary sociality as 1, matrilineal lineages but no male care as 2, monogamous species as 3, and communal groups with cooperative foraging as 4 (as in Swihart et al., 2003). Niche breadth was an ordinal value from 0 to 3 as calculated by the sum of a mammal's specialization across three axes, diet, denning, and locomotion. For each of these three traits, mammals received a 0 if they were a generalist and a 1 if they were a specialist. A generalist was defined as possessing an omnivorous diet, terrestrial locomotion, and terrestrial or fossorial denning (Laurance, 1994; Swihart et al., 2003; Viveiros de Castro & Fernandez, 2004; Prugh et al., 2008), and a specialist was anything else.

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Statistical Analyses

To assess the predictive value of potential growth rate, mass, home range, and niche breadth, we used linear regressions. Potential growth rate, mass, and home range were continuous variables and niche breadth was an ordinal variable. Since land managers frequently do not know all five life histories for a given species, and since the goal of this research is to inform management, we regressed the effect statistic ($-\beta_1$ from Eq. 1) against each predictor individually. To assess possible inverse trends within order, we evaluated individual scatterplots with each taxonomic order. We also regressed the effect statistic against life histories for each taxonomic order represented by at least 10 species. Investigation of Cook's distance revealed fitted values with an influence greater than the 20th percentile for potential growth rate, mass, and home range. Thus we log-transformed these predictors (Kutner et al., 2005), and each of the regressions were as in the following equation:

$$\text{effect} \sim \beta_0 + \beta_1 * \text{life history} \qquad \text{(Eq. 2)}$$

We also compared ordinary linear models to linear mixed-effects models within which the individual slopes and intercepts were allowed to vary according to taxonomic order. Visual investigation of effect values as predicted by sociality revealed a discernible break point as differentiated by an absence (0, 1, 2) or presence (3, 4) of male care for offspring. To assess whether the presence or absence of male care predicted the effect of fragmentation on mammalian abundances, we performed a Wilcoxon rank sum test. All statistical analyses were run in R 2.10.1 (R Development Core Team, 2009).

Results

All five life history traits had a significant impact on the predicted effects of fragmentation on mammalian abundances. Higher potential growth rates reduced the impact of habitat fragmentation (*Table 2, Fig. 1a*; positive correlation with effect statistic), and species with paternal care were more negatively affected by fragmentation than those without paternal care (*Fig. 1b*; Wilcoxon rank sum, W = 2947.5, $p = 0.017$).

Table 2. *Effect of fragmentation on mammalian abundances as predicted by life history traits. Below are results from the linear regression of the effect statistic against each predictor as in equation 2.*

predictor	β_1	**(±SE)**	***p*-value**	R^2
log (potential growth rate)	0.0209	(0.0062)	0.001	0.054
log (mass)	-0.0119	(0.0045)	0.009	0.029
log (home range)	-0.0100	(0.0043)	0.022	0.029
niche breadth	-0.0678	(0.0259)	0.009	0.030

Mass, home range, and niche breadth all showed significant negative correlations with the effect statistic (*Table 2*), indicating that species with heavier mass, larger home

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range, and greater degree of specialization had lower abundances in habitat fragments (*Fig. 1c, d, e*).

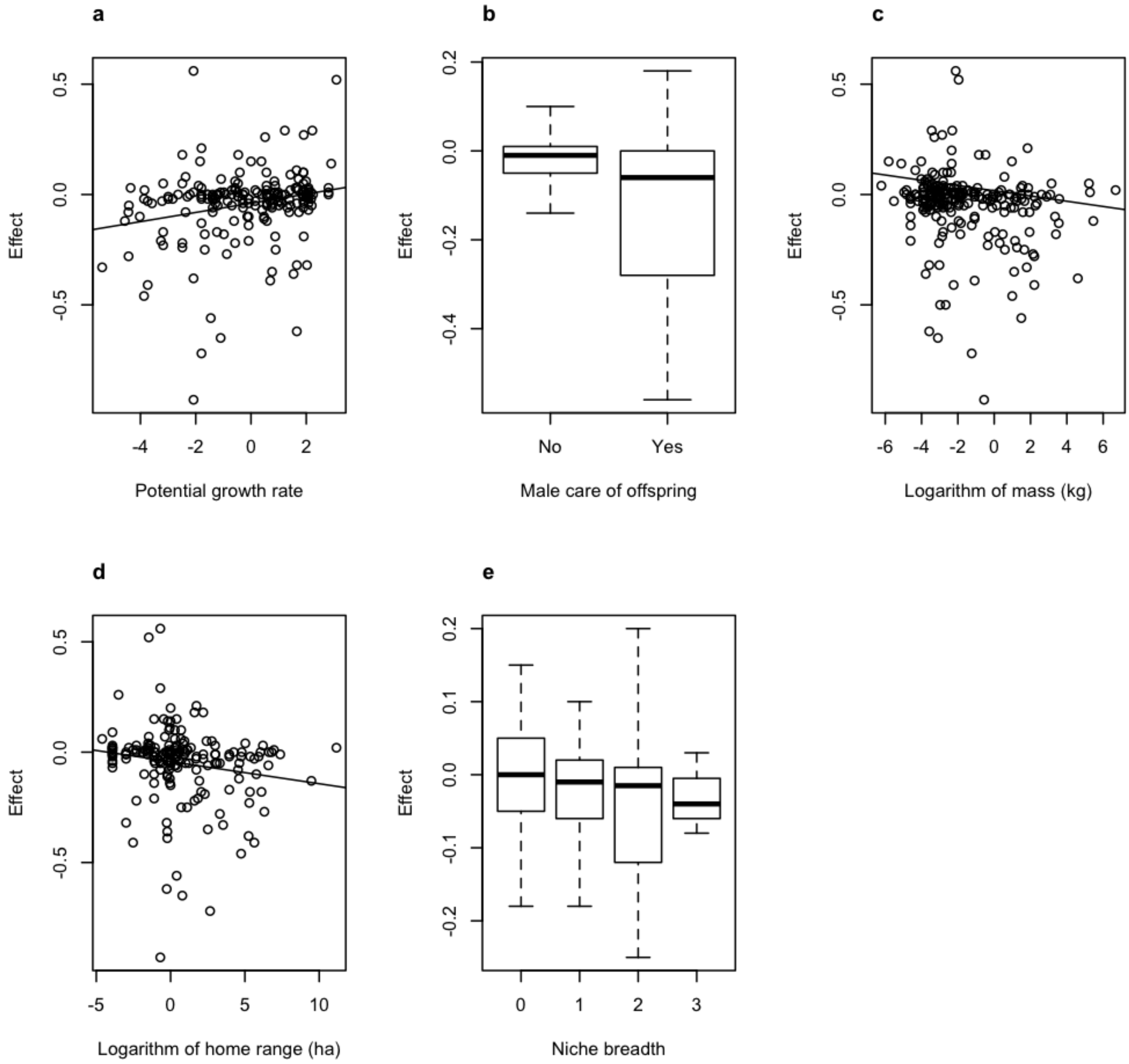

Figure 1. *Effect of fragmentation on mammal abundances as predicted by (a) potential growth rate, (b) mammals with and without paternal care, (c) mass, (d) home range, and (e) increasing specialization across niche breadth.*

The addition of taxonomic order as a random effect did not alter the interpretation of the results. With all five of the life histories, the coefficient and standard error for each regression changed less than 0.0003 with the addition of order as a random effect.

Linear regressions of the effect of fragmentation against life histories within taxonomic orders containing greater than 10 species revealed no significant trends (*Table 3*). We found no inverse trends within any of the five life history predictors indicating the trends found were not caused by over representation of any one order.

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Discussion

In accordance with previous predictions, all five life history traits predicted mammalian abundances across a gradient of habitat fragmentation, and each of these correlations were significant. Thus the theorized tenets of mammalian life history as applied to the impacts of fragmentation appear sound, and generalizations found in a host of more specific studies appear to be substantiated by this meta-analysis.

Potential growth rate has been shown to correlate with Australian mammal abundances across a fragmented landscape, where species with lower growth rates had lower abundances in habitat fragments and vice versa (Laurance, 1991). Our research also indicates that mammals that are slow to mature and have few offspring are most likely to experience declines due to fragmentation (*Table 2, Fig. 1a*).

Social mammals can respond to fragmentation differently than asocial species. For example, the tree hyrax (*Dendrohyrax arboreaus*) and blue duiker (*Philantomba monticola*) do not exhibit parental care and had gradual declines due to fragmentation whereas the samango monkey (*Cercopithecus mitis*) has parental care and experienced dramatic declines in abundance (Lawes et al., 2000). The differences in abundances across these species were attributed to their social structure (Lawes et al., 2000). Our meta-analysis supports the observation that mammals with paternal care are more negatively affected by fragmentation than those without (*Fig. 1b*).

Several studies have found that larger mammals have lower abundances in habitat fragments than smaller species. In the Brazilian Atlantic forest, five common mammals of mass greater than 1 kg had average densities in 20,000 ha habitat fragments nearly triple that found in 200 ha fragments (Chiarello, 2000). On the Sunda shelf islands of Indonesia and Malaysia mammals of large body sizes were absent from smaller islands (Okie & Brown, 2009). Body size also accounts for carnivore abundances across coastal southern California with larger species having lower abundances in habitat fragments (Crooks, 2002). In the Chiquitano forests of Bolivia, mammals with a body mass less than 6 kg were found to have greater abundances in habitat fragments than in contiguous forests (Kosydar, 2010). Our results agree that mammals of greater mass are more susceptible to fragmentation (*Table 2, Fig. 1c*).

Mammals with larger home ranges need larger habitat fragments in order to support viable populations. Since people hunt mammals, the edges of habitat fragments can serve as a sink, thus rendering species with wide ranges especially susceptible to fragmentation (Woodroffe & Ginsberg, 1998). A study of ten carnivores found that mammals with large home ranges are more likely to go extinct than mammals with small home ranges (Woodroffe & Ginsberg, 1998). We found that this trend appears to hold true across taxa and that species with larger home ranges have lower abundances in fragmented habitats (*Table 2, Fig. 1d*).

The conservation literature points out differing responses of specialists and generalists to fragmentation. For example, a meta-analysis of amphibians, reptiles, invertebrates, birds and mammals in habitat fragments found that the specialization of diet and locomotion could predict the presence or absence of a species (Prugh et al., 2008). Results from the Biological Dynamics and Forest Fragments Project indicated that generalist herbivores and omnivores have stable or increasing abundances, whereas specialist predators have declined (Laurance et al., 2002). In Queensland, Australia specialization along the axes of diet, denning, and locomotion strongly correlated with abundances of five mammals with specialists nearly extirpated from habitat fragments (Laurance, 1990). The results of this meta-analysis indicate that resource specialization

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in general – spanning all three of these axes – indicates a species response to fragmentation (*Table 2, Fig. 1e*).

Table 3. *The effect of fragmentation as predicted by life histories within mammalian orders with at least 10 species represented.*

order	potential growth rate		sociality		mass	
	β_1 (±SE)	*p*-value	W	*p*-value	β_1 (±SE)	*p*-value
Carnivora	-0.05 (0.06)	0.41	5	0.50	-0.01 (0.01)	0.93
Cetartiodactyla	-0.03 (0.05)	0.55	12	0.36	-0.01 (0.03)	0.80
Didelphimorphia	-0.04 (0.07)	0.59	no paternal care		-0.04 (0.02)	0.11
Diprotodontia	-0.05 (0.13)	0.69	10	1.00	0.04 (0.08)	0.66
Eulipotyphlya	0.02 (0.01)	0.10	no paternal care		-0.01 (0.01)	0.46
Primates	-0.01 (0.06)	0.82	11	0.43	0.00 (0.05)	0.92
Rodentia	0.01 (0.01)	0.24	308	0.54	-0.02 (0.01)	0.15

order	home range		niche breadth	
	β_1 (±SE)	*p*-value	β_1 (±SE)	*p*-value
Carnivora	0.01 (0.03)	0.80	0.06 (0.08)	0.50
Cetartiodactyla	0.00 (0.02)	0.96	-0.04 (0.10)	0.72
Didelphimorphia	-0.04 (0.02)	0.08	0.03 (0.07)	0.70
Diprotodontia	0.00 (0.15)	0.98	0.13 (0.20)	0.54
Eulipotyphlya	-0.01 (0.01)	0.67	0.01 (0.05)	0.81
Primates	-0.02 (0.04)	0.65	0.03 (0.09)	0.74
Rodentia	-0.01 (0.01)	0.60	-0.06 (0.04)	0.09

The above findings must be interpreted with care. Given that the trends we found were across taxonomic orders and not within taxonomic orders, we suggest that in the absence of additional research, these results should not be used to compare species within one order. Secondly, although we found a significant effect of fragmentation on abundances and we predicted this effect based upon a mammal's potential growth rate, sociality, mass, home range, and niche breadth, we also found a large degree of stochasticity with each of these predictors. Thus these results are best interpreted as suggestive of a mammal's potential response to fragmentation. Yet the stochasticity is not random. Given that we attempted to make global generalizations across a wide taxonomic array, a large amount variation should be expected.

Our findings indicate that the previously proposed theories generally hold and that each of the five life histories correlated with a mammal's response to fragmentation. For managers attempting to assess which mammals are most susceptible to habitat fragmentation, these life history traits can serve as a predictive tool. When developing plans about which species to monitor, this framework is likely to yield results allowing managers to focus limited resources on mammals that are prone to declines, specifically,

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mammals with slow growth rates, paternal care, large mass, wide home ranges, and specialized niches. These five life history traits could provide a relative risk index that managers could use to help predict changes in abundances due to habitat fragmentation.

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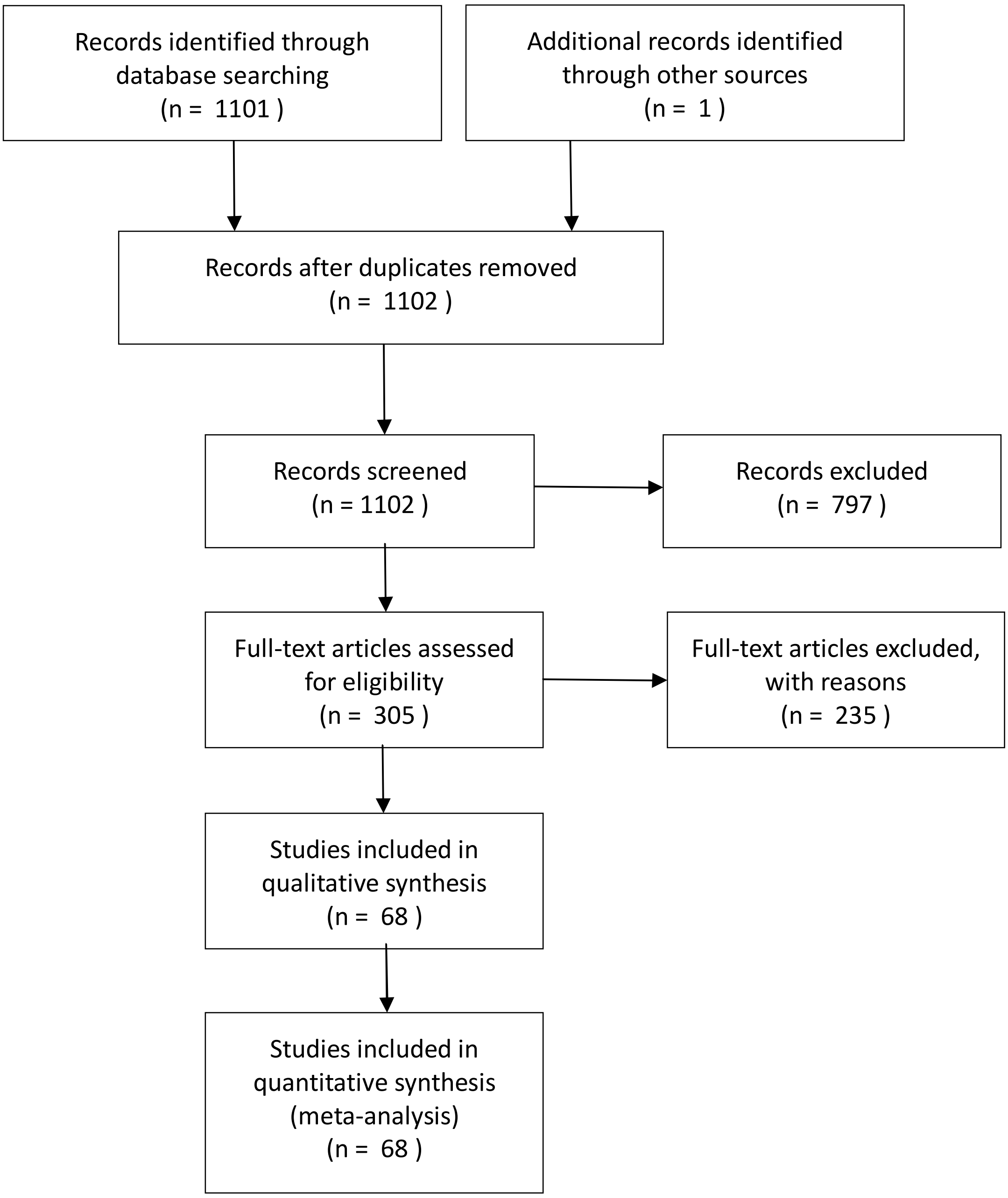
Appendices

Appendix 1. *PRISMA Flow Diagram (Moher et al., 2009) detailing the flow of information through the different phases of the meta-analysis. This flow diagram maps out the number of records identified, included and excluded, and the reasons for exclusions.*



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Appendix 2. *List of 68 studies from which data was extracted for the meta-analysis. An asterisk (*) in front of the title indicates that the author(s) of the study shared additional data for inclusion in this meta-analysis.*

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