species by fitting broken-stick regressions to these data. Activities such as the initiation of panting (**$T_b$ panting initiated**) and any signs of stress were noted. Measurements were terminated and birds were removed from the respirometry chamber if they exhibited prolonged escape behaviour (jumping, pecking and/or wing flapping) or if clearly distressed (loss of coordination/balance or a sudden drop in EWL, RMR and/or an uncontrolled increase in $T_b$. A bird was considered to have reached its upper limit of heat tolerance at the $T_{air}$ associated with the onset of these signs of heat stress and/or if $T_b$ increased uncontrollably. This was considered the heat tolerance limit (**HTL**) of the individual (Whitfield *et al.* 2015).

In addition, I used EWL data extracted from the studies summarised in Table 1 to model water requirements, by predicting EWL over hourly intervals to obtain estimates of cumulative EWL on the hottest day measured during the 2015 Kalahari field season (as had been previously calculated for a subset of nine of the 20 species; Chapter 3). I expressed these cumulative water requirements as a percentage of body mass lost as EWL during an 8-h period during the hottest day experienced (**EWL as Percentage Mass**).

### 4.3.4 *Data analysis*

Czenze *et al.* (2020) recently showed that passerines which drink surface water display greater evaporative scope and higher HTLs than those which obtain all their water from food. I therefore including drinking dependence alone and in interaction with each physiological predictor variable in models of $pant_{50}$. As data were missing for physiological variables related to $T_b$ ($T_{air}$ of $T_b$ inflection, $T_b$ panting initiated) for six species (see Table 1), I fitted two separate candidate model sets, and compared models within them using Akaike's Information Criterion, adjusted for small samples

(Symonds & Moussalli 2011, Harrison *et al*. 2018). Firstly, I omitted the two variables for which data were missing and compared a model set of the null model, drinking dependency, each physiological variable alone and each variable and the interaction with drinking dependency (n = 20 species). Secondly, I omitted six species for which data was missing and included all physiological variables and compared outputs of the same model set as mentioned above (n = 14 species).

I also examined my dataset for differences in evaporative scope and HTL among the 13 passerines compared to values reported by Czenze *et al.* 2020. I used simple linear models with drinking/non-drinking as a predictor and evaporative scope and HTL as response variables.

I report results in text as (LM: estimate [L95%CI – U95%CI]). Where multiple models were within ΔAICc = 2.0 of the top model, top model sets were averaged using the package MuMin (Barton 2015) and parameter estimates after model averaging were presented for interpretation (Burnham & Anderson 2002, Grueber *et al.* 2011). For all analyses, I visually inspected residuals to ensure model assumptions were met. Statistical significance of the effects of retained predictor variables was inferred if 95% confidence intervals (CIs) excluded zero.

## 4.4 Results

$Pant_{50}$ was not correlated with drinking dependency or any of the physiological variables examined (Figure 1), with the null model included in the top model set for the analysis including all 20 species (null model ΔAICc = 0.06; n = 20, Table 2A), 2A), and representing the top model for the analysis including the subset of species for which additional $T_b$ variables were available (n = 14 species, Table 2B).

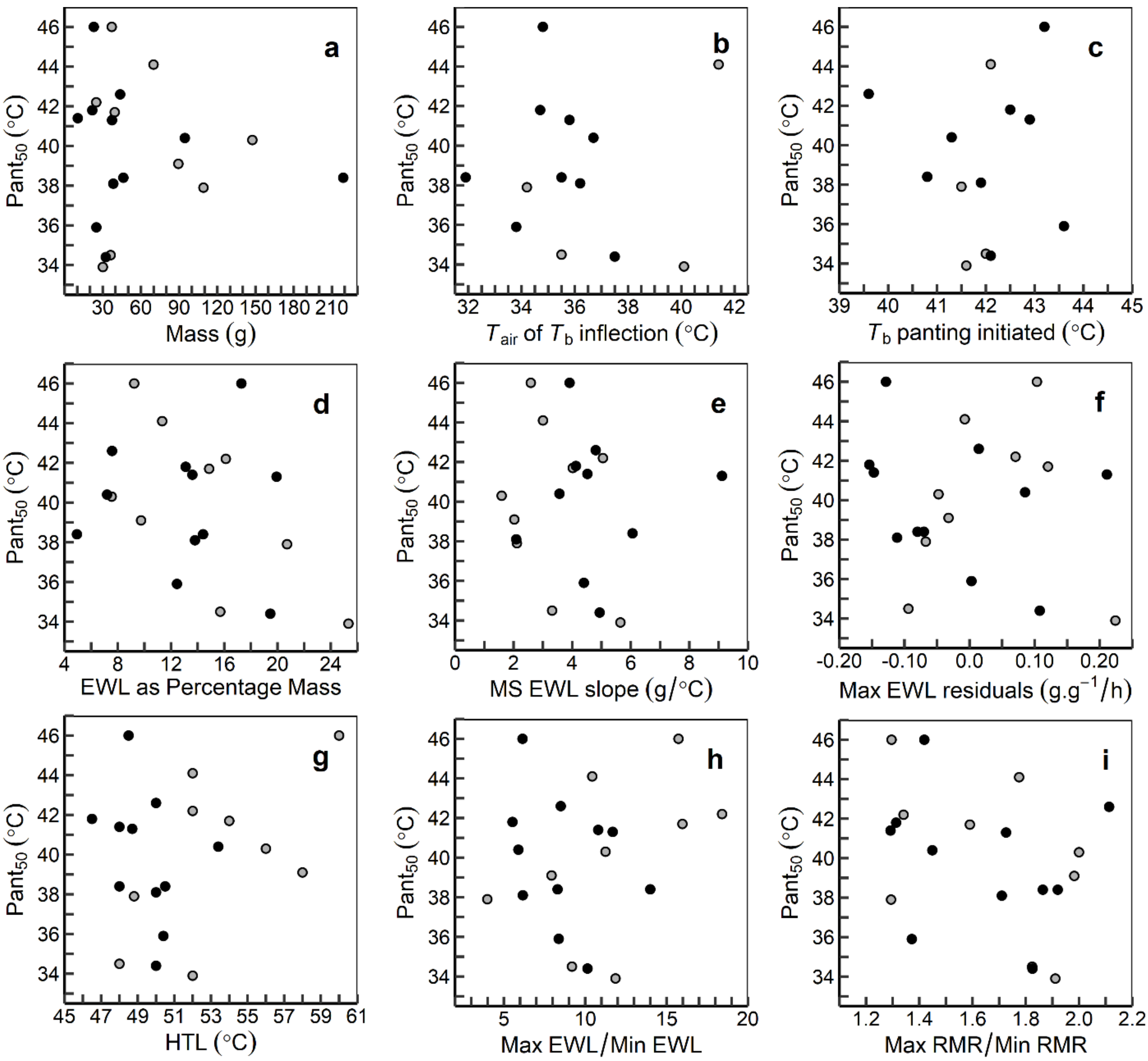


**Figure 1**: $Pant_{50}$ was not correlated with any of the physiological variables I included in the analysis. I used the residuals of the log linear relationship of Max EWL against body mass (to account for differences in EWL with body mass), in the $pant_{50}$ analysis of Max EWL. Drinking dependent species are indicated using black filled circles and non-drinking species by grey filled circles.

Cumulative EWL as a percentage of body mass, metabolic cost index (Max RMR/Min RMR) and HTL were included in competing models within ΔAICc = 2 for analysis of all 20 species (Table 2A). However, these variables had no significant relationships with $pant_{50}$ after model averaging (95% CIs include 0 in all cases; Table

**Table 2:** Top GLMM models predicting $pant_{50}$ for all analyses, ranked by AICc. Models within ΔAICc < 2 were considered competing models. Significance is inferred if 95% CIs (LCI-UCI) exclude zero.

| ***A. Candidate model set excluded physiological variables*** $T_{air}$ ***of*** $T_b$ ***inflection and*** $T_b$ ***panting initiated, n = 20 species*** | **AICc** | **ΔAICc** | **Weight** | |
|---|---|---|---|---|
| $pant_{50}$ ~ Percent EWL of Mass | 111.09 | 0.00 | 0.18 | |
| $pant_{50}$ ~ | 111.15 | 0.06 | 0.18 | |
| $pant_{50}$ ~ Max RMR/Min RMR | 111.51 | 0.42 | 0.15 | |
| $pant_{50}$ ~ HTL | 112.67 | 1.57 | 0.08 | |
| *Effect size of explanatory variables after model averaging* | **Estimate** | **SE** | **LCI** | **UCI** |
| Percent EWL of Mass | -0.25 | 0.16 | -0.56 | 0.07 |
| Max RMR/Min RMR | -4.31 | 3.02 | -10.23 | 1.62 |
| HTL | 0.25 | 0.25 | -0.23 | 0.73 |

| ***B. Candidate model set included physiological variables*** $T_{air}$ ***of*** $T_b$ ***inflection and*** $T_b$ ***panting initiated, n = 14 species*** | **AICc** | **ΔAICc** | **Weight** | |
|---|---|---|---|---|
| $pant_{50}$ ~ | 80.78 | 0.00 | 0.25 | |
| $pant_{50}$ ~ Percent EWL of Mass | 82.14 | 1.37 | 0.13 | |
| *Effect size of explanatory variables after model averaging* | **Estimate** | **SE** | **LCI** | **UCI** |
| Percent EWL of Mass | -0.24 | 0.18 | -0.61 | 0.15 |

Cumulative EWL as a percentage of body mass was also included in a competing model for the analysis of 14 species, but again was not significant after model averaging (Table 2B).

Evaporative scope was significantly higher in drinking passerines compared to non-drinkers (LM: estimate = 5.98 [2.24 - 9.72], n = 13) as was HTL (LM: estimate = 3.41 [1.65 – 5.18], n = 13).

## 4.5 Discussion

I found no correlations between $pant_{50}$ and any physiological variables linked to thermoregulation and heat tolerance in arid-zone birds, with null models performing better or competing with top models in all analyses. These findings provide no support for my predictions that $pant_{50}$ could reliably indicate changes in thermal physiology during exposure to hot weather, or heat tolerance limits. There are several potential explanations for this puzzling finding.

First, by including data from orders that vary in their primary avenues of evaporative heat dissipation, I may have obscured within-order patterns. Passerines rely largely on panting for evaporative cooling, a metabolically costly and comparatively inefficient process (Dawson 1982, McKechnie *et al.* 2021*a*), whereas many non-passerine orders use gular flutter, the rapid movement of the gular membranes driven by pulsation of the hyoid apparatus. Gular flutter provides rapid evaporation at much lower metabolic costs compared to panting (Bartholomew *et al.* 1962). Furthermore, columbiforms also use transdermal cutaneous evaporative water loss to effectively and rapidly dissipate heat at negligible metabolic expense (Dawson & Whittow 2000). To assess whether phylogenetic variation in primary evaporative cooling pathways was driving the results, I repeated analysis on passerines alone. After excluding non-passerines, however, the results remained unchanged (Table S2 & S3). Among southern African passerines, regularly-drinking species that rely on surface water have higher evaporative scope (i.e., maximum

EWL / minimum EWL) and higher heat tolerance limits compared to non-drinking species that balance water budgets using dietary and metabolic water (Czenze *et al.* 2020). Further, in the Kalahari Desert, drinking-dependent species have significantly lower $pant_{50}$ (Smit *et al.* 2016). I therefore predicted that $pant_{50}$ may correlate at an interspecific level with HTL and evaporative scope, with low $pant_{50}$ associated with higher HTL and a greater evaporative scope. The fact that the null models performed better than models including either HTL or evaporative scope and drinking dependency is therefore surprising, particularly within the passerines (Table S2 and S3). My results were consistent with those of Czenze *et al.* 2020 in that drinking passerines exhibited higher HTL and evaporative scope, whereas I found no difference in $pant_{50}$ among drinking and non-drinking passerines. Therefore, while drinking dependence may be functionally related to HTL and evaporative scope among passerines, $pant_{50}$ is apparently not.

Second, although the onset of panting and rapid increases in EWL are widely thought to coincide with the upper critical limit of thermoneutrality ($T_{uc}$), recent evidence suggests that there may be considerable variation in relationships between $T_b$, EWL and RMR towards the upper end of the TNZ and at $T_{air} > T_{uc}$. The $T_{uc}$, the inflection of RMR at the upper boundary of the thermoneutral zone, is thought to represent the energetic cost of heat dissipation mechanisms such as panting (Dawson & Whittow 2000). However, the relatively weak relationship between $T_{air}$ at the onset of panting and the inflection of EWL with $T_{uc}$ among arid-zone passerines from three continents (McKechnie *et al.* 2021) suggests this is not necessarily the case. Further, the inflection $T_{air}$ at which $T_b$ begins to increase is often below the $T_{uc}$. Therefore, the fact that $T_{uc}$ is a poor indicator of increases in RMR and EWL, and that these variables are only weakly correlated with the $T_{air}$ at the onset of panting

(McKechnie *et al.* 2021) and the $T_{air}$ inflection at which $T_b$ increases, suggests that there is considerable variation in the relationship between increases in RMR or EWL and panting behaviour. Given the amount of noise in these relationships, it is unlikely that $pant_{50}$ will accurately reflect physiological heat responses based on these variables.

A third possibility explaining the absence of clear links between $pant_{50}$ and physiological variables arises because I examined $pant_{50}$ independently of other thermoregulatory behaviours. In a subset of nine of the species used in this study, the combination of thermoregulatory behaviours (e.g. reductions in activity, increased shade-seeking and increased panting), and physiological mechanisms (e.g. facultative hyperthermia), birds used to thermoregulate effectively in the heat was clearly species-specific (Thompson *et al.* 2018). Similarly, the order in which these behaviours commenced was also species-specific. Therefore, one would need to understand how each species utilises shade-seeking, wing drooping and reductions in activity to complement $pant_{50}$ in order to accurately use these behaviours to predict when physiological heat dissipation is necessary. In addition, when the captive birds involved in the aforementioned study were subjected to restricted water availability, thermoregulatory responses varied substantially between and even within avian orders, with each species regulating $T_b$ using a unique combination of these behavioural and physiological mechanisms to cope with dehydration. As such, although several species delayed panting until higher $T_{air}$ when dehydrated, presumably to conserve water, interpretation of interspecific variation in $pant_{50}$ needs to take place in the context of interactions with other thermoregulatory behaviours, including increased shade-seeking and reductions in activity (Thompson *et al.* 2018) and hydration state (Chapter 2).

Pattinson *et al.* (2020) quantified interspecific variation in heat dissipation behaviour (HDB; including panting, shade-seeking, wing-drooping and activity reduction) across three phylogenetically disparate avian communities inhabiting the Gascoyne Desert in western Australia, the Sonoran Desert in the southern USA and the Kalahari Desert in southern Africa. Although the range of interspecific variation was similar among regions, very little variation in HDB was predicted by organismal traits including body mass, drinking dependency, foraging guild, diet and activity levels. The lack of a relationship between $pant_{50}$ and body mass in the current study is broadly consistent with these findings, as is the absence of any relationship between $pant_{50}$ and drinking dependency. This once again highlights the complexity of interspecific variation in HDB.

In summary, my results here suggest $pant_{50}$ is not suitable as a predictor of avian physiological heat responses or thermal tolerance limits. However, while the risk of exposure of arid-zone avian communities in southern Africa to lethal, acute effects of heat exposure via lethal dehydration or hyperthermia is predicted to remain low in the 21$^{st}$ century (but see McKechnie *et al*, 2021*b*), chronic sublethal fitness costs, often associated with missed foraging opportunities due to trade-offs with behavioural thermoregulation at high air temperatures, are predicted to increase dramatically (Conradie et al 2019, Cunningham *et al* 2021). Sublethal fitness costs include progressive loss of body mass in adults, reduced breeding success, and reduced nestling growth resulting in smaller, lighter fledglings (Du Plessis *et al.* 2012, Cunningham et al 2013, Van de Ven *et al.* 2019, Conradie *et al.* 2019, van de Ven *et al.* 2020). Poor-quality offspring fledged from heat-exposed nesting attempts are likely to be less successful breeders as adults due to the strong correlation between future breeding success and mass at fledging and therefore these effects persist intergenerationally (Ridley & Raihani 2007, Ghalambor & Martin 2001, Weimerskirch *et al.* 2000). These chronic sublethal costs may be a more pervasive threat to avian diversity in southern Africa's hot, desert environments than acute physiological heat responses and thus, predicting vulnerability to these costs may be more important.

Although less invasive than physiological data collection, collecting data on fitness consequences for species existing in these environments is time-consuming, requiring years of data collected across numerous seasons. $Pant_{50}$ might serve no purpose in predicting vulnerability of avian communities to climate change based on physiological tolerances, but there is a possibility that it may predict vulnerability to the sublethal fitness consequences to rising temperature. Although speculative, preliminary data from Southern Pied Babblers and Southern Yellow-billed hornbills tentatively suggest a correlation between $pant_{50}$ and $T_{air}$ thresholds of diurnal mass gain but many more species will need to be included to elucidate these links.

Therefore, I recommend that future studies examine the value of $pant_{50}$ as predictor of vulnerability to sublethal fitness costs, e.g. via correlations with threshold $T_{air}$s above which a) food intake is not enough to offset overnight mass loss, b) probability of breeding success drops below 50% and c) impacts on nestling growth and fledging mass are felt, among others. In addition, further research is required to identify $T_b$ thresholds at which panting, shade-seeking and reductions in activity take place, requiring fine scale monitoring of $T_b$. This could increase the efficiency with which we can predict the impacts of sublethal fitness costs of high $T_{air}$ across avian desert communities, enabling targeted conservation action for the species most vulnerable.

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## 4.7 Appendix

**Table S1:** Complete model set outcomes

*A. For all species with variables $T_{air}$ of $T_b$ inflection and $T_b$ panting initiated omitted (n = 20).*

| Models | AICc | ΔAICc | Weight |
|---|---|---|---|
| $pant_{50}$ ~ Percent EWL of Mb | 111.09 | 0.00 | 0.18 |
| $pant_{50}$ ~ | 111.15 | 0.06 | 0.18 |
| $pant_{50}$ ~ Max RMR/Min RMR | 111.51 | 0.42 | 0.15 |
| $pant_{50}$ ~ HTL | 112.67 | 1.57 | 0.08 |
| $pant_{50}$ ~ Max EWL/Min Ewl | 113.22 | 2.13 | 0.06 |
| $pant_{50}$ ~ Max EWL resid | 113.72 | 2.63 | 0.05 |
| $pant_{50}$ ~ Mb | 113.78 | 2.69 | 0.05 |
| $pant_{50}$ ~ Drink | 113.79 | 2.69 | 0.05 |
| $pant_{50}$ ~ MS EWL slope | 113.87 | 2.78 | 0.05 |
| $pant_{50}$ ~ Drink : Max RMR/Min RMR | 113.90 | 2.81 | 0.05 |
| $pant_{50}$ ~ Drink : Percent EWL of Mb | 114.23 | 3.14 | 0.04 |
| $pant_{50}$ ~ Drink : HTL | 115.81 | 4.72 | 0.02 |
| $pant_{50}$ ~ Drink : Max EWL/Min EWL | 115.99 | 4.90 | 0.02 |
| $pant_{50}$ ~ Drink : Max EWL resid | 116.25 | 5.16 | 0.01 |
| $pant_{50}$ ~ Drink : Mb | 116.76 | 5.66 | 0.01 |
| $pant_{50}$ ~Drink : MS EWL slope | 117.03 | 5.94 | 0.01 |

*B. For all variables including $T_{air}$ of $T_b$ inflection and $T_b$ panting initiated and omitting six data deficient species (n = 14).*

| Models | AICc | ΔAICc | Weight |
|---|---|---|---|
| $pant_{50}$ ~ | 80.78 | 0.00 | 0.25 |
| $pant_{50}$ ~ Percent EWL of Mb | 82.14 | 1.37 | 0.13 |
| $pant_{50}$ ~ Max EWL resid | 82.93 | 2.15 | 0.09 |
| $pant_{50}$ ~ Max EWL/Min Ewl | 83.17 | 2.40 | 0.08 |
| $pant_{50}$ ~ Max RMR/Min RMR | 83.57 | 2.79 | 0.06 |
| $pant_{50}$ ~ Tair of Tb inflection | 83.92 | 3.14 | 0.05 |
| $pant_{50}$ ~ Drink | 83.92 | 3.15 | 0.05 |
| $pant_{50}$ ~ HTL | 83.97 | 3.19 | 0.05 |
| $pant_{50}$ ~ Tb panting initiated | 84.07 | 3.29 | 0.05 |
| $pant_{50}$ ~ MS EWL slope | 84.09 | 3.31 | 0.05 |
| $pant_{50}$ ~ Mb | 84.09 | 3.31 | 0.05 |

| | | | |
|---|---|---|---|
| $pant_{50}$ ~ Drink : Percent EWL of Mb | 85.64 | 4.86 | 0.02 |
| $pant_{50}$ ~ Drink : Max EWL resid | 86.96 | 6.18 | 0.01 |
| $pant_{50}$ ~ Drink : Max EWL/Min EWL | 87.17 | 6.39 | 0.01 |
| $pant_{50}$ ~ Drink : Max RMR/Min RMR | 87.61 | 6.84 | 0.01 |
| $pant_{50}$ ~Drink : MS EWL slope | 87.78 | 7.00 | 0.01 |
| $pant_{50}$ ~ Drink : Tair of Tb inflection | 87.87 | 7.10 | 0.01 |
| $pant_{50}$ ~ Drink : HTL | 87.92 | 7.14 | 0.01 |
| $pant_{50}$ ~ Drink : Tb panting initiated | 87.95 | 7.17 | 0.01 |
| $pant_{50}$ ~ Drink : Mb | 88.12 | 7.34 | 0.01 |

**Table S2:** Top GLMM models for predicting $pant_{50}$ for passerine species, ranked by AICc. Significance is inferred if 95% CIs (LCI-UCI) exclude zero.

| ***A. Excluding physiological variable $T_{air}$ of $T_b$ inflection and $T_b$ panting initiated, n = 13*** | **AICc** | **ΔAICc** | **Weight** |
|---|---|---|---|
| Null model | 72.7 | 0 | 0.44 |
| *Top competing models* | | | |
| $pant_{50}$ ~ Percent EWL of Mass | 73.4 | 0.7 | 0.31 |
| [LM: $F_{1,11}$ = 2.61, t = -1.61, $p$ = 0.13] | | | |
| ***B. Three species missing data removed, n = 10*** | **AICc** | **ΔAICc** | **Weight** |
| Null model | 59.7 | 0.0 | 0 |
| *No competing models* | | | |

**Table S3:** Complete model set outcomes

*A. For all passerines with variables $T_{air}$ of $T_b$ inflection and $T_b$ panting initiated omitted (n = 13).*

| **Models** | **AICc** | **ΔAICc** |
|---|---|---|
| $pant_{50}$ ~ | 72.7 | 0.0 |
| $pant_{50}$ ~ Percent EWL of Mass | 73.4 | 0.7 |
| $pant_{50}$ ~ Max EWL resid | 75.0 | 2.3 |
| $pant_{50}$ ~ Max RMR/Min RMR | 76.0 | 3.3 |
| $pant_{50}$ ~ Max EWL/Min EWL | 76.0 | 3.3 |
| $pant_{50}$~ Mb | 76.0 | 3.3 |
| $pant_{50}$ ~ HTL | 76.0 | 3.4 |
| $pant_{50}$ ~ MS EWL Slope | 76.1 | 3.5 |
| $pant_{50}$ ~ Drink | 76.1 | 3.5 |
| $pant_{50}$ ~ Drink + Percent EWL of Mass | 77.7 | 5.0 |

| | | |
|---|---|---|
| $pant_{50}$ ~ Drink + Max EWL resid | 79.0 | 6.3 |
| $pant_{50}$ ~ Drink + HTL | 80.2 | 7.6 |
| $pant_{50}$ ~ Drink + Max RMR/Min RMR | 80.3 | 7.6 |
| $pant_{50}$ ~ Drink + Mb | 80.3 | 7.6 |
| $pant_{50}$ ~ Drink + Max EWL/Min EWL | 80.3 | 7.6 |
| $pant_{50}$ ~ Drink + MS EWL Slope | 80.5 | 7.8 |

*B. For all variables including $T_{air}$ of $T_b$ inflection and $T_b$ panting initiated and omitting three data deficient species (n = 10).*

| **Models** | **AICc** | **ΔAICc** |
|---|---|---|
| $pant_{50}$ ~ | 59.7 | 0.0 |
| $pant_{50}$ ~ Percent EWL of Mass | 61.8 | 2.1 |
| $pant_{50}$ ~ Max EWL resid | 62.5 | 2.8 |
| $pant_{50}$ ~ HTL | 63.1 | 3.4 |
| $pant_{50}$ ~ Max EWL/Min EWL | 63.7 | 4.1 |
| $pant_{50}$ ~ Tair of Tb inflection | 63.8 | 4.2 |
| $pant_{50}$ ~ Drink | 63.9 | 4.2 |
| $pant_{50}$ ~ Max RMR/Min RMR | 63.9 | 4.2 |
| $pant_{50}$ ~ Tb panting initiated | 63.9 | 4.3 |
| $pant_{50}$ ~ Mb | 63.9 | 4.3 |
| $pant_{50}$ ~ MS EWL Slope | 63.9 | 4.3 |
| $pant_{50}$ ~ Drink : Percent EWL of Mass | 67.8 | 8.1 |
| $pant_{50}$ ~ Drink : Max EWL resid | 68.4 | 8.8 |
| $pant_{50}$ ~ Drink : HTL | 69.0 | 9.3 |
| $pant_{50}$ ~ Drink : Max EWL/Min EWL | 69.7 | 10.0 |
| $pant_{50}$ ~ Drink : Tair of Tb | 69.8 | 10.1 |
| $pant_{50}$ ~ Drink : MS EWL Slope | 69.8 | 10.2 |
| $pant_{50}$ ~ Drink : Max RMR/Min RMR | 69.9 | 10.2 |
| $pant_{50}$ ~ Drink : Mb | 69.9 | 10.2 |
| $pant_{50}$ ~ Drink : Tb panting initiated | 69.9 | 10.2 |