

Jelle Loonstra  
Bachelor Thesis  
University of Groningen (RUG)  
Biology – Ecology and Evolution  
Mentor: Prof. dr. J.M. Tinbergen

# **Personalities and risk taking behaviour?**

## Abstract

Since behavioural biologists found evidence that behaviour of individuals is much less flexible than previously thought (R'eale et al. 2007) evolutionary and theoretical biologists developed theories how personalities evolve and how different personality traits coexist in one population (Dingemanse et al. 2010). In this thesis I collect empirical evidence for the model that Wolf et al. 2007 introduced. His model suggests that personality traits are related to differences in risk-taking behaviour. Variation in individual prospects should co vary with risk taking behaviour causing some individuals to show risk prone and other risk aversive behaviour types. I found evidence for this theory in the Namibian rock Agama (Carter et al. 2010), Bluegill-sunfish (Wilson et al. 2009), sticklebacks (Bell. 2006) and wild fiddler crabs (Reaney et al. 2007), but not in great tits (Van Oers et al. 2004), European house crickets (Wilson et al. 2010) and sticklebacks (Bell 2006). In other words there are studies that show a correlation in the occurrence of risky-personality traits within a species, but other studies don't. This thesis concludes that the relation between different risk-taking behavioural traits is not yet clear. The ecological context influences the correlation between risky-behavioural traits and future research has to provide answers on a more quantitative basis.

## Contents

<b>Introduction</b> .....	<b>4</b>
What are animal personalities?.....	4
How did personalities evolve?.....	4
What is risk-taking behaviour?.....	5
<b>Empirical evidence for correlations between risky personality traits</b> .....	<b>6</b>
Wild fiddler crabs, <i>Uca mjoebergi</i> .....	6
Great tit, <i>Parus major</i> .....	6,7
Namibian rock agama ( <i>Agama planiceps</i> ) .....	7,8
European house cricket ( <i>Acheta domesticus</i> ) .....	8,9
Bluegill sunfish ( <i>Lepomis macrochirus</i> ) .....	9
Sticklebacks ( <i>Gasterosteus aculeatus</i> ).....	10
<b>Discussion</b> .....	<b>11,12</b>
Reference.....	13,14

## Introduction

*This thesis is a follow up on my bachelor-research, which I have done on personalities in Great Tits. We investigated whether male aggressiveness influences their fitness. That project raised my interest in personalities and is the reason why I write my bsc-thesis about 'personalities and risk-taking behaviour'.*

### *What are animal personalities?*

When you are watching any group of people, you will see that there are individual differences in behaviour. Individuals differ consistently in different aspects of their behaviour. You may see differences in aggressiveness towards others, in exploration of new environments and in several other behavioural components. These differences in behaviour, are well studied in humans (Pervin et al. 1999) but less so in animals. Since Huntingford did her pioneering work on three-spined sticklebacks (Huntingford 1976), consistent differences in animal behavior were not longer ignored (Sih et al. 2004). Today consistent individual differences in behaviour across situations are called personalities (Gosling 2001). Since Huntingford's work, personalities were documented in a wide range of animal species (Sih et al. 2004). Traits that exhibit consistent individual differences include aggressiveness, shyness-boldness, exploration-avoidance, activity and sociability (R'eale et al. 2007). By what we know today, different questions arise: How did personalities evolve? and Why do different personalities coexist? In this thesis I will discuss the adaptive explanation that Wolf et al. (2007) gave. Their idea is that individuals differ in fitness expectation and as a consequence may differ in risk-taking behaviour (Wolf et al. 2007).

This thesis discusses the idea that personality is correlated with risk-taking behaviour. First I will review studies that measured a suite of correlated behavioural traits to see whether interpretation along the risk-taking axis makes sense. Finally, I will discuss the consistency between the empirical data and the theory and give suggestions for further research.

### *How did personalities evolve?*

Since behavioural biologists found evidence that behaviour of individuals is much less flexible than previously thought (R'eale et al. 2007) evolutionary and theoretical biologists developed theories how personalities evolve and how different personality traits coexist in one population (Dingemanse et al. 2010). In this thesis I will collect empirical evidence for the model which Wolf et al. introduced (Wolf et al. 2007). This model suggests that personality traits are related to differences in risk-taking behaviour. From Caraco et al. we know that differences in risk-taking behaviour is related to differences in future fitness-expectation (Caraco. 1981). Individuals with a high fitness-expectation should be than relatively risk-averse and individuals with low fitness-expectations should be risky in their behaviour, because they have less to lose. Consequently this suggests that there is a relation between risk-taking and personality traits (figure 1), what means that individuals with a personality at one end of the scope are risk-prone in all their personality -components and that individuals on the other end of the scope risk-averse are in all their components. This is

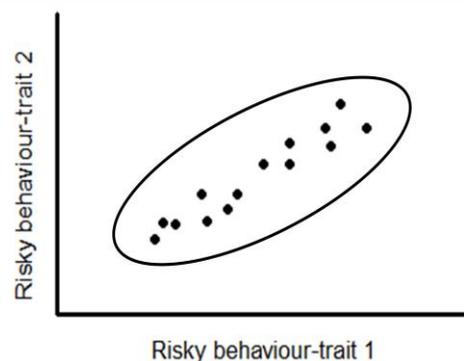


Figure 1. Theory suggest that risky-behaviour traits should correlate within individuals (Wolf et al, 2007)

because all the risk-taking personality-components are a product of the fitness-expectation of that individual and should be consistent among these trait. In literature a relationship between two different personality types within an individual is called a behavioral syndrome (Sih et al. 2004). So, in this thesis I will emphasize the idea that personality are correlated with risk taking behaviour. Because personalities are suites of correlated behaviours, we would expect that slow individuals will be risk averse and fast individuals risk prone.

#### *What is risk-taking behaviour?*

Risk-taking behaviour is for the first time described by Caraco (1981). He describes risk-taking behaviour in dark-eyed juncos (*Junco hyemalis*) in relation to their hunger-status. The birds in this experiment, had experience with two situations that differed in the chance to obtained food. In situation (1) they always obtained 10 food items and in the other situation (2) they could obtain 20 food items but the chance that they got nothing was 50%. In both situations the expectation was that the birds obtained on average the same amount of food items, but the variance in intake between the two situations differed. Caraco, tested birds in two different states, either hungry or not-hungry. What he discovered was that hungry birds took more risks and preferred situation (2), while the satiated birds preferred situation (1) were they always obtained food. Towards a good explanation why variance is favored in hungry birds we have to cast the problem in terms of survival probabilities. For the satiated birds, 10 food items are enough to survive the night, but for the hungry birds, it might be not enough to survive the night, yet 20 food items may. So it is worth to take the risk for the hungry bird to choose the patch with the highest variance, because even when the 10 food items appear with certainty it may not be enough to survive the night.

This risk-sensitive theory predicts that birds in a good condition should choose for the not-risky situation, while birds that are not in a good condition should choose the option with the highest variance, but also with the greatest risks. Extending this idea to the coexistence of personalities, variation in behaviour can perhaps be explained by individual differences in long-term fitness-expectation, because this difference could lead to a difference in risk-taking behaviour.

## Empirical evidence for correlations between riskiness of personality traits

During the past few years, the number of studies on personalities and behavioural syndromes has been increasing (R'eale et al. 2010). This gives the opportunity to summarize studies where different personality traits have been studied. Here, I will discuss six different studies (Van Oers et al. 2004; Wilson et al. 2010; Wilson et al. 2009); Reaney et al. 2007; Carter et al. 2010; Bell 2006). From these studies I will outline how personality-traits relate to each other and how we can interpret each personality trait in terms of risk-taking. To scale the personalities in risk-taking I also will discuss the ecological context, because the context it is essential for the interpretation in terms of risk taking.

In wild fiddler crabs, *Uca mjoebergi*, Reaney et al. (2007) studied two different behaviours of males, risk-taking and occupying a new burrow (aggression) (Reaney et al. 2007). Risk-taking behaviour was quantified as re-emergence time after an attack of a potential predator. As potential predator an artificial model bird was used, because the common sandpiper was observed to be the most important predator. Fiddlers were classified by re-emergence time, in bold (<25sec) and shy (>50sec). Aggressiveness was quantified by the time to occupy a burrow. The crabs were placed in a new environment where they had three options to gain a new burrow: (1) fight a resident male, (2) evict a female and (3) occupying an empty burrow. To scale these personality-traits into

categories of risk-taking, the context of these behaviours is important. The first trait, re-emergence time after a potential predator-attack is risky, expecting the chance that a fiddler is being predated after an attack is higher when he re-emerge quicker. Occupying a new burrow can also be quantified as risk-taking it has been shown that fighting with another male for a burrow gives more risks than occupying an empty burrow or gaining a burrow from a female (Archer 1988; Groothuis 2011). All experiments were done in the natural habitat, so effects of non-natural conditions on the behaviour were not expected (Bell 2006; Wright et al. 2006). In figure 2 the results of this experiment are shown. Bolder fiddlers (high-risk takers) evict more males for a new burrow than shy males (low-risk takers). The latter were more likely to evict a burrow from a female or occupy an empty burrow, which is less risky. This result shows a positive relation between risky personality traits within individuals, consistent with the hypothesis of Wolf et al. (2007).

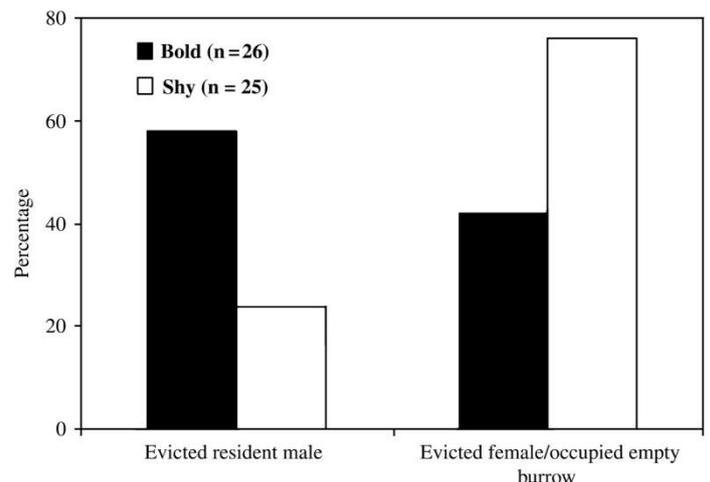


Figure 2. The percentage of bold and shy males that either fought a territorial male for a new burrow or avoided fights by evicting a female or occupying an empty burrow. Graph: (Reaney et al. 2007)

The relation between exploratory behaviour and risk-taking behaviour was also studied in the great tit (*Parus major*). Van Oers et al. (2004) measured two different personality traits: (1) Exploration, measured by a novel-object test and a novel-environment test, (2) risk-taking, measured by the startle latency test. With the startle latency test the birds were observed in a room and were startled by a plate which was managed by the observer. Measured was the time that an individual took the first mealworm after a startle. We have to interpret these traits in terms of risk-taking. Explorative birds can be seen as risk-taking birds. Because if an individual is more willing to explore a new environment or object, the chance that he is confronted with a unexpected risky situation, is greater. The second measurement can be defined as risky by casting the trait in survival probabilities. Birds that take their food quicker after a startle, obtain a greater risk because the danger is likely to be nearer still,. Birds with a shorter latency obtain more risks to be predated than the birds that wait. In figure 3, the two risky-behaviours (risk-taking and exploratory behaviour) are plotted. Van Oers et al. found no significant relationship ( $r_p = 0.45$ ,  $n=15$ ,  $p=0.09$ ), but there was a trend that slow explorers (risk-averse) did have a longer startle latency than those who are fast explorers (risky).

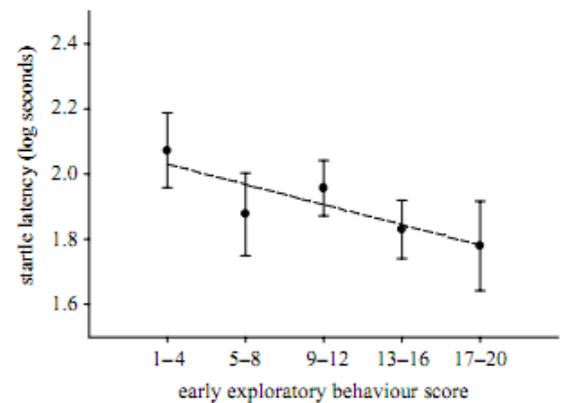


Figure 3. Mean startle latency with early exploratory behaviour. Graph: (Van Oers et al., 2004)

In another study on the wild Namibian rock agama, *Agama planiceps*, (Carter et al., 2010) two different personality traits were observed. (1) Flight initiation distance, measured as the distance which an individual ran when it was approached by a predator. (2) Proportion of time spent conspicuous, this trait includes the time which an individual spent prominent basking and moving while signaling. Beside these personality traits home range and the tail length were also measured from each individual. Males that fled when the predator is closer can

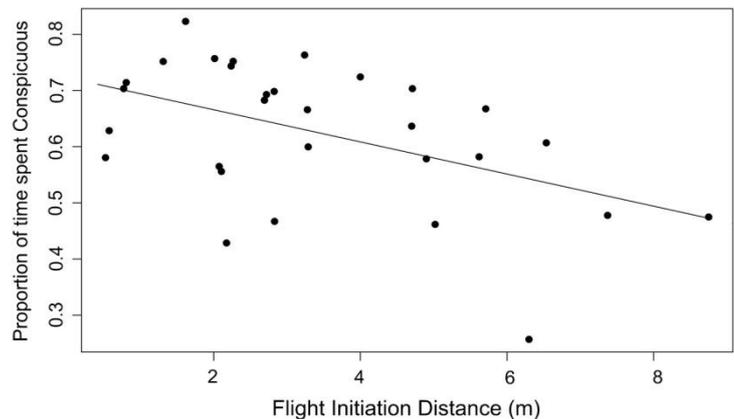


Figure 4. The relationship between male FIDs and the proportion of time spent in Conspicuous Behaviors (basking and moving) Graph: (Carter et al. 2010)

be called risk takers, assumed that when you are closer to a predator the chance that you will be eaten is increased. The second trait can also be interpret as a risky-trait, because when a male is moving while signaling and prominent basking, the chance that he will be predated is greater (Carter et al. 2010). In this study (fig 4) Carter et al. found that individuals that have a shorter fleeing distance (risky) also spent more time conspicuous (risky) ( $\beta \pm SE = 16.63 \pm 4.29$ ,  $df = 26$ ,  $t = 23.87$ ,  $P = 0.006$ ). Individuals show, consistent risk-taking behaviour across different contexts.

Carter et al. found evidence that the flight initiation distance relates to risky behaviour, by studying the relation between individual flight initiation distance and the tail length. Individuals with a low flight initiation distance lost a larger piece of their tail. This relation could be due to the lower flight initiation distance which has led to a greater chance of being attacked. But the relation between

these traits can also be caused by a reduced fitness, caused by an attack, which led than to a reduced flight initiation distance.

A lot of personality research has been done in insects. Here I discuss a study from Wilson et al. (2010) on the European house cricket, *Acheta domestica*. Wilson et al. observed six different personality traits (table 1). Before discussing the correlating between the different traits, I will discuss the risk-taking component of each trait. The first trait, activity, has been recognized in literature as an ecologically relevant measure of risk taking (Wilson et al. 2005; Sih et al. 2004). Antipredator behaviour, is also suggested to be risky by arguing that differences in behaviour towards a predator increases the chance to be predated (Dugatkin 2010). Exploration/silent can in this experiment seen as a risky trait if we assume that new objects or environments are risky. The reaction on the sound made by another individual can differ between individuals and affects risk taking. For example individuals that make more sound are more likely to be predated (Wilson et al. 2010). Behaviour related to mate extraction can also be classified as risk-taking, because song can attract predators and increases the risk to be predated (Wilson et al. 2010).

Activity	Walking forwards
	Climbing
	Turning arround
	Walking backwards
Antipredator	Latency to emerge following predation threat
	Latency to autotomize limb
	latency to emerge post automy
Exploration/Silent	Latency to emerge in novel silent environment
	Latency to touch object in novel silent environment
Mating/Exploration	Latency to emerge in novel phonotaxis environment
	Latency to touch speaker in novel phonotaxis environment
Mate attraction	Calling bout rate (bouts/24h)
	Bout lenght
Aggression	Grappling
	Mandible flare
	Biting
	Chirping

Table 1. The measured behaviours from Wilson et al., 2010

Wilson et al. also measured aggression. Predators can also be attracted by this sound. In general I reason that behaviour like movement and sound production increases the detectability for a predator and is therefore more risky. Also how animals perform when a predator is close by, or how they react to novel environments can be related to risk taking in this way.

To see if risk-taking behaviours were associated within individuals, the measured behaviours were correlated. In table 2 the correlation between behaviours is shown. Males, who were more explorative, called more than the less explorative males. More exploratory females exhibited stronger responses to male mating calls than less exploratory females. Also, explorative individuals in both sexes were more willing to emerge quickly following a predation event. These result show that risky traits are *not* always correlated within individuals. This raises the question why this is so? One explanation could be, that this population of European house crickets was domesticated for many generations and thereby lost their natural behaviour (Bell 2006). In that case the results are worthless. Another reason could be that judge risk wrongly because we do not know the biology of

the species well enough. To verify this explanation, riskiness has to be quantified and not inferred as we do now.

Sex	Trait 1	Trait 2	All individuals included		
			R <sub>s</sub>	P-value	N
Male	Exploration/silent	Mate attraction	-0,3109	0,0066	71
female	Exploration/silent	Mating/exploration	0,2793	0,0096	85
Male	Exploration/silent	Antipredatory	0,3080	0,0090	71
female	Exploration/silent	Antipredatory	0,2805	0,0093	85

Table 2. The significant positive correlations between the measured behaviours. (Wilson et al. 2010)

Behavioural research has a strong history in fish (Conrad et al. 2011). Here I discuss a study from Wilson et al. (2008) on bluegill sunfish (*Lepomis macrochirus*). Wilson et al. investigated the relationship between three different behavioral traits: (1) Activity, defined as the total time spent swimming during a 10-min observation period (2) Risk-taking, measured by a combination of the time spent close to a predator, the time spent inspecting the predator and the time spent in the upper water zone (3) Exploratory behaviour, defined as latency to emerge from refuge and latency to touch the new object. Also in this example I will discuss how each behavioural trait relates to risk taking. For trait (1) where the activity of each individual was measured, I interpret this as an ecologically relevant measures of risk-taking (Sih et al. 2004; Wilson et al. 2007). Trait (2) measured different behavioural aspects directly related to predation, and thus to risk taking (Sih et al. 2004; Lima et al. 1990). In guppies it was shown that a higher predator inspection rate, increases the chance to be predated (Dugatkin 2010). The last trait (3) can be related to risk-taking by assuming that explorative individuals are risk-prone, because individuals that are more willing to explore a new environment or object, are expected to have a greater chance to be confronted with a risky situation. Important to mention is that an individual is explorative when it has a low score on the exploration-axis (short latency time). The correlation structure between these behaviors (figure 5) shows that individuals that are explorative, meaning that they have a short latency time, were also more active and more willing to inspect a potential predator and spent more time in risky areas. In this study risk-taking behavior does differ between individuals, and it is consistent within individuals among different traits consistent with the idea of Wolff.

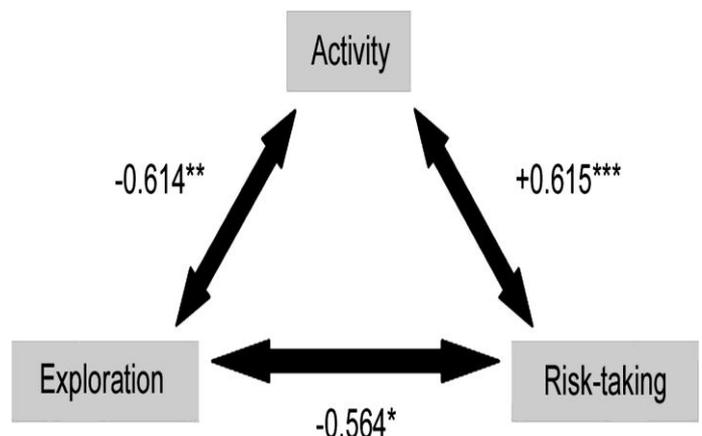


Figure 5. Behavioural syndrome showing correlations between 3 component behaviours (activity, exploration and risk taking) in bluegill sunfish (Wilson et al., 2008).

To show that correlations between different personalities depend on the ecological context, Bell (2006) repeated the study of Huntingford (1976). But in contradiction to Huntingford she took for her experiment sticklebacks (*Gasterosteus aculeatus*) from two populations that differed in predation pressure. Each individual was scored for two behavioural traits, (1) Aggression, measured by the number of bites to a conspecific and the time spent with a conspecific (2) Boldness, measured by the time spent foraging in a risky situation and the latency to do that. Aggression can be defined as risky, because interactions between individuals can be costly (and therefore more risky) by so called losing-effects (Groothuis 2011). The second trait boldness, can be related to risk taking by arguing that foraging under predation risk can be risky through a greater chance to be predated (Dugatkin 2010). As an extra note, the aggression tests were done between fish from the same sub-species and the same body size.

Results showed that ecological context mattered. Individuals from the population experiencing high predation-risk behaved like they did in the study of Huntingford. But in the population with low predation risk, no relationship was found between aggressiveness and boldness. Comparing the personality traits between the two populations, individuals from the population with a higher predation risk were more aggressive towards intruding conspecifics, than those that lived in a population where the predation-pressure was lower (Mann–Whitney  $U=345$ ,  $P < 0.01$ ,  $n = 71$ ). Individuals from the population with a low predation-pressure were more active and willing to incur predation risk in order to gain food (Mann–Whitney  $U = 286$ ,  $P < 0.0001$ ,  $n = 71$ ). These results show that relations between behavioural components differ between populations that differ in ecological context. In this case, I suggest that predation pressure might be a key-factor for the difference in behaviour. To verify this, further research is needed.

## Discussion

The aim of this thesis was to see whether empirical data were consistent with the theoretical hypothesis from Wolf et al (2007) (Van Oers et al. 2004; Wilson et al. 2010; Wilson et al. 2009); Reaney et al. 2007; Carter et al. 2010; Bell 2006). Wolf suggested that personality, defined as suites of behavioral traits that co vary within individuals, may be explained by the asset protection hypothesis. If so individuals should consistently differ in their risk taking behaviour. The question in this thesis was: Is there empirical evidence that individuals consistently differ in risk taking behavior and that this explains correlations between the occurrence of behaviours (figure 1)? Summarizing I cannot give a clear conclusion because patterns differ between studies.

In crabs, Namibian Rock agama's, sticklebacks and the blue gill-sunfish I found a positive relation between the risk taking aspects of different behavioral traits. This means that individuals with a personality at one end of the scope are risk-prone in all their behaviors and that individuals on the other end of the scope risk-adverse are in all their components. This supports Wolffs' hypothesis who argues that individuals should display consistent risk-taking behaviour. But, in European house crickets, Great tits and Sticklebacks I found no clear positive correlation in the risk taking aspects of different behavioral traits. This difference in relationships between risk taking aspects of different behavioral traits, can be explained by three different explanations: (1) differences in ecological context (2) domestication effects and (3) problems with quantifying risky traits.

First of all, looking at the two populations of sticklebacks who differ in predation pressure (Bell 2006), we saw that there was a difference in the relation between the risk taking aspects of different behavioral traits (Bell 2006). This suggests that ecological conditions, especially predation pressure, may play a role in the determination of associations between risky behavioural traits.

Another effect which I point out in table 3 is that populations that are domesticated for many generations show another relation between risky behavioural traits than populations that are not domesticated. Domesticated populations did not show a relation between behavioural traits, but in the studies where animals from natural populations were used a positive correlation between risky behavioural traits did exist. Also from previous research it is known that domestication can influence the behaviour of an individual (Wright 2006).

Studies	Tests were done with a natural population	Tests were done with a domesticated population	Positive relation between risky-behavioural traits
Reaney et al. 2007	+	-	+
Van Oers et al. 2004	-	+	-
Carter et al. 2010	+	-	+
Wilson et al. 2009	+	-	+
Wilson et al. 2010	-	+	+/-
Bell 2006	+	-	+/-

Table 3 Shown is here the relation between risky behavioural traits of natural populations and domesticated populations

The last explanation why risk taking aspects of different behavioral traits might not be consistent, is that in none of the studies actual risk have been quantified. I used an interpretation of the riskiness of a behaviour. Advice for future research is to get a more quantitative insight in the riskiness of behavioural traits.

I can conclude that there are studies that show, when individuals are compared, a positive correlation between risky personality traits, but other studies don't. This result is not consistent with the hypothesis of Wolff, that predicted a positive relation between risk taking behavioural traits. This thesis suggests that the relation between risk-taking behavioural traits is not always present. I show that ecological context and domestication effects influence the correlation between risky-behavioural traits. Most and for all this may be caused by the fact that riskiness has to be measured in the ecological context rather than inferred from general principles. Likely a certain behaviour is risky in one but not in another context. Therefore it is far too early to reject Wolfs hypothesis.

## References

- Pervin, L.A. & John, O.P. (1999) Handbook of Personality: Theory and Research. New York: The Guilford Press.
- Huntingford, F.A. (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behavior* **24**, 245-260
- Gosling, S.D. (2001) From mice to men: What can we learn about personality from animal research? *Psychological Bulletin* **127**, 45-86
- Sih, A; Bell, A.M.; Johnson, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends In Ecology & Evolution* **19**, 372-378
- R'éale, D; Reader, S.M.; Sol, D. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291-318
- Wolf, M; Van Doorn, G.S.; Leimar, O; Weissing, F.J.; (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**, 581-584
- Archer, J (1988) The behavioural biology of aggression. Cambridge: Cambridge University Press
- Dingemanse, N.J.; Wolf, M (2010) Recent models for adaptive personality differences: a review. *Philosophical Transactions Of The Royal Society B-Biological* **365**, 3947-3958
- Caraco, T (1981) Energy budgets, risk and foraging preferences in dark-eyed Juncos (*Junco hyemalis*). *Behavioral Ecology And Sociobiology* **8**, 213-217
- Sih, A; Bell, A.M.; Johnson, J.C. (2004) Behavioral syndromes: An integrative overview. *Quarterly Review Of Biology* **79**, 241-277
- R'éale, D; Dingemanse, N.J.; Kazem Anahita, J.N. (2010) Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions Of The Royal Society B-Biological* **365**, 3937-3946
- Van Oers, K; Drent, P.J.; de Goede, P. (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings Of The Royal Society Of London Series B-Biological Sciences* **271**, 65-73
- Wilson, A.D.M.; Whattam, E.M.; Bennet, R. (2010) Behavioral correlations across activity, mating, exploration, aggression and antipredator contexts in the European house cricket, (*Acheta domesticus*). *Behavioral Ecology And Sociobiology* **64**, 703-715
- Wilson, A.D.M.; Godin, J.J.; (2009) Boldness and behavioral syndromes in the bluegill sunfish, (*Lepomis macrochirus*) *Behavioral Ecology* **20**, 231-237
- Reaney, L.T.; Backwell, P.R.Y. (2007) Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behavioral Ecology* **18**, 521-525
- Carter, A.J.; Goldizen, A.W.; Tromp, S.A. (2010) Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology* **21**, 655-661

Bell, A.M. (2006) Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal Of Evolutionary Biology* **38**, 484-473

Wright, D.; Nakamichi, R.; Krause, J.; Butlin, R.K. (2006) QTL analysis of behavioral and morphological differentiation between wild and laboratory zebrafish (*Danio rerio*). *Behavioral Genetics* **36**, 271–284

Groothuis, A.G.G. (2011) Aggressio. Lecture 'Behavioural biology'

Conrad, J.L.; Weinersmith, K.L.; Brodin, T.; Saltz, J.B.; Sih, A (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal Of Fish Biology* **78**, 395-435

Wilson, A.D.M.; Stevens E.D. (2005) Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology* **111**, 849-862

Wilson, A.D.M.; McLaughlin, R.L. (2007) Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*. **74**: 689-698

Lima, S.L.; Dill, L.M.; (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* **68**, 619-640.

Dugatkin, L.A. (2010) Principles of animal behavior. London. W.W. Norton & Company