

**Banff International Research Station** 

# for Mathematical Innovation and Discovery

# Inclusive Fitness Workshop 10w5017 Sunday June 13 to Friday June 18

# MEALS

\*Breakfast (Buffet): 7:00 – 9:30 am, Sally Borden Building, Monday – Friday
\*Lunch (Buffet): 11:30 am – 1:30 pm, Sally Borden Building, Monday – Friday
\*Dinner (Buffet): 5:30 – 7:30 pm, Sally Borden Building, Sunday – Thursday
Coffee Breaks: As per daily schedule, 2nd floor lounge, Corbett Hall
\*Please remember to scan your meal card at the host/hostess station in the dining room for each meal.

# **MEETING ROOMS**

All lectures will be held in Max Bell (Max Bell Building accessible by walkway on 2nd floor of Corbett Hall). LCD projector, overhead projectors and blackboards are available for presentations. *Note that the meeting space designated for BIRS is the lower level of Max Bell, Rooms 155-159. Please respect that all other space has been contracted to other Banff Centre guests, including any Food and Beverages in those areas.* 

# SCHEDULE

	Monday	Tuesday	Wednesday	Thursday	Friday
7:00 - 9:30	Buffet Breakfast, Sally Borden Building				
8:45 - 10:15	Sta. Manager	Grafen	Rousset	Wild	Presentation/
Max Bell 159	Intro (Taylor)	Whitlock	Lion/Jansen/Day	Ubeda	Discussion
	Queller	Foster	Alizon	Alonzo	
	Gardner				
10:15 - 10:45	Coffee Break, 2nd floor lounge, Corbett Hall.				
10:45 - 12:00	Discussion	Discussion	Discussion	Discussion	Wrap up
Max Bell 156					end at 11:15
12:00 - 13:30	Buffet Lunch, Sally Borden Building				
13:30 - 15:00	1:00 Tour	Presentation/	free for walks	Presentation/	Checkout by
Max Bell 156	2:00 Photo	Discussion	and climbing	Discussion	12 pm.
	Presentation				TRAVEL
14:45 - 15:150	Coffee Break			Coffee	HOME
15:15 - 16:15	Discussion	Discussion		Discussion	
Max Bell 156					
17:30 - 19:30	Buffet Dinner, Sally Borden Building				

Check-in begins on Sunday June 13 at 16:00(Front Desk - Professional Development Centre - open 24 hours). Buffet Dinner (17:30-19:30), Sally Borden Building. Lecture rooms available after 16:00. Informal gathering in 2nd floor lounge after 20:00, Corbett Hall, where beverages and a small assortment of snacks are available on a cash honor system.

On Monday June 14th at 8:45 the BIRS Station Manager will make introduction and welcome remarks in Max Bell 159.

A free guided tour of The Banff Centre is offered to all participants and their guests on Monday starting at 1:00 pm. The tour takes approximately 1 hour.

A group photo will be taken on Monday at 2:00 pm. Please meet on the front steps of Corbett Hall.

We will break for lunch at 11:15 on Friday to facilitate those who need to catch the 12:30 shuttle to Calgary Airport. Participants are welcome to use BIRS facilities (2nd Floor Lounge, Max Bell Meeting Rooms, Reading Room) until 3 pm on Friday, although you are required to checkout of the guest rooms by 12 noon.

# Preliminary Abstracts for BIRS Inclusive Fitness Workshop. June 2010.

### Samuel Alizon.

"Incorporating kin selection into evolutionary epidemiology"

#### Suzanne Alonzo

I will centre my talk on current ideas I am working on and things I find worth thinking about for the future. I am very focused at present in thinking about we how we can model social interactions and sexual selection in a strong evolutionary framework without losing behavioral complexity and plasticity.

## **Kevin Foster**

"Inclusive fitness in real cell groups"

One of the goals of my group is to apply inclusive fitness logic to microbial groups, which we do with a mix of analytical approximations, individual based models and then real bacterial colonies. Because the organisms we study are relatively simple, the hope is to make strong links between the theory and the behavior of the organisms themselves. While qualitative predictions on the effects of relatedness are feasible, however, quantitative predictions are difficult. This is in part due to familiar difficulties with costs and benefits, but also with assessing the relevant spatial scales of social action. Looking to the future, therefore, one question I am very interested in is the extent to which one can marry general inclusive fitness models with those that make predictions based on the detailed biology of each particular system.

## Andy Gardner, Stu West & Geoff Wild

#### The genetical theory of kin selection.

Natural selection operates through the impact of a trait upon the reproductive success of its bearer (direct fitness) and the impact of the trait upon the reproductive success of genetically-related social partners (indirect fitness). The net effect of natural selection is summarized by Hamilton's rule, rb-c > 0, which represents the sum of direct and indirect fitness effects, and provides the core result of social evolution theory. A number of studies have questioned the generality and validity of Hamilton's rule, suggesting that it is only a heuristic result or requires that specific assumptions be made. Here, we use Fishers genetical paradigm to clarify the generality of Hamilton's rule and to form links between different studies. We show that misconceptions regarding Hamilton's rule have arisen owing to confusion of: (1) the cost and benefit terms in Hamilton's rule with arbitrary model parameters; (2) the coefficient of genetic relatedness in Hamilton's rule with degree of genotypic similarity or genealogical relationship; and (3) general theory with streamlined methodology developed for ease of analysis.

## Alan Grafen:

How to reconcile inclusive fitness as studied by theoreticians and as employed by field biologists?

I would probably like to discuss the contrast between the approach of my 2006 inclusive fitness paper and those of the dynamically sufficient models that others construct; from the point of view of the "take-home message" we would like non-theoreticians to understand about inclusive fitness.

Further comments: I would like the (or maybe a) focus of the workshop to be: to what extent does theory support the views of general biologists about inclusive fitness?

This involves (i) saying something about what those views actually are (ii) what theory currently shows absolutely in a (iia) positive and (iib) negative light about those views and (iii) on that basis what a reasonable guess is about the general validity of those views. These exercises would (1) be important for general biologists, to be informed about what theory currently says for sure and what it might plausibly say in the future and (2) be important for theoreticians, in drawing attention to those issues that deserve further work because of their significance for applications.

The different strands of fundamental work seem to me to make this program a very timely and useful one. It must be remembered that inclusive fitness maximisation, across a broad range of environmental variation, geographical structure, and conditional and complex behaviour, is currently taken for granted across much of whole organism biology, and is the basis for a great deal of field work, and for grants awarded for field work. Yet the strength of the theoretical support for that position is not clear.

### Sebastien Lion, Vincent Jansen and Troy Day

"Inclusive fitness theory for complex/realistic ecological dynamics?"

#### **David Queller**

Joint effects, non-additivity, frequency-dependence, and greenbeards

The inclusive fitness method gains power and clarity by attributing all fitness effects to the individual that caused them. Complications arise when fitness effects are caused by the joint actions of more than one individual. This is not a rare case, but includes all frequency dependence and most situations covered by game theory. Mathematically, one way of putting it is that fitness effects are non-additive, and this is a well-recognized difficulty for inclusive fitness theory. On the conceptual side, there is also a problem. Inclusive fitness effects are commonly divided into those that affect kin, and greenbeard effects that specifically target shared alleles. Joint effects occur only when the partner shares the allele. We need to either recognize these as greenbeard effects, or enlarge our conceptual scheme beyond kin and greenbeards.

#### **Francois Rousset**

Title: Inclusive fitness in population-genetic and data-analytic perspectives.

Abstract: Nearly all of us may agree that inclusive fitness theory provides a wonderful set of tools for an ever-increasing understanding of the natural world. I will speculate on the minimal way these concepts can be profitably explained to both theoreticians and non-theoreticians. Some examples of unanswered problems will help define the current limits of the approach, which are limits of theoretical population genetics rather than of inclusive fitness theory per se. I will explain what motivates my approach through examples about which we may have different views, such as possible discrepancies between population genetic and inclusive fitness approaches, relatedness concepts under isolation by distance, and the pros and cons of a narrow definition of inclusive fitness. Communicating the minimal set of concepts is impeded by real-life constraints, as (among other reasons) it does not fit comfortably within simplistic but better-diffused versions of game theory, inclusive fitness, and data-analytical concepts. I dream that the participants will solve all these communication problems.

#### Francisco Ubeda:

Inclusive fitness and intragenomic conflict. [Renamed from Kin selection and intragenomic conflict!]

#### **Michael Whitlock**

I would describe the methods I've used to model evolution in a discrete-population spatial context. I'd apply it to evolution on recessive alleles to show the origin, but show also how this can be used for other frequency dependent processes like social evolution. I think there are two other points that I would also try to squeeze in: (1) a demonstration that frequency - dependent evolution can lead to group-level processes even in the absence of kin-structure (an old point, but perhaps one that could be profitably made in this era of re-definiton), and (2) a brief discussion about how lattice models usually assume far too extreme dispersal limitation (relative to real populations), making their conclusions a bit overblown.

My whole approach only applies to discrete populations structure, and it is limited to weak selection. It does however apply to relatively general models of population structure.

#### **Geoff Wild**

Inclusive fitness from multitype branching processes (turning plastic into gold).

Branching processes provide a link between inclusive fitness and the probability of extinction of a mutant allele. In particular, branching processes help us to formalize "plastic standard" inclusive fitness analyses, putting these on par with their "gold standard" cousins. I will briefly outline a branching-processes approximation of a version of the Wright-Fisher model, and I will show how inclusive fitness pops out of this. I will also show how numerical analysis and simulation of branching processes allows us to extend analyses beyond the "weak selection" domain.